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W. BATESON, M.A., F.R.S.

DIRECTOR OF THE JOHN INNES HORTICULTURAL INSTITUTION

AND

R. C. PUNNETT, M.A., F.R.S.

ARTHUR BALFOUR PROFESSOR OF GENETICS IN THE UNIVERSITY OF CAMBRIDGE

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STUDIES ON PAPILLARY PATTERNS OF HUMAN FINGERS

By KRISTINE BONNEVIE,
Institut for Arvelighetsforskning, University of Kristiania, Norway.

(With 37 Text-figures, 24 Tables and 4 Plates.)

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Introduction[1].

An important series of facts seems to prove beyond doubt the heredity of finger-patterns. Demonstration of such heredity and especially any attempt at genetical analysis are made most difficult by the existence of the following complications:

(a) Complications arising from the fact that the inherited factors carried by one developing individual show their effects upon no less

[1] Throughout the text and tables the word "finger" is used in the sense of "digit." Thus "first finger" means the thumb, "second finger" the index, and so on. The apical pads presenting the patterns are spoken of as "finger-balls," for which there is no exact English equivalent.

than ten fingers, which, as we soon learn, very seldom develop their patterns in the same way.

This fact makes it necessary to find means of comparing and summing up the patterns of all ten fingers in order to get some expression representing the characteristics of the whole individual. A method of doing so will be demonstrated in this paper.

(*b*) Complications arising from the fact, easily demonstrated, that each of the ten fingers differs from all the others with regard to the statistical frequency with which it presents the several types of finger-patterns.

Until the causation of this peculiar fact is properly understood, no full appreciation of its genetical significance is attainable. Upon this point much is still left for further investigation, not only of the digits of different human races, but also those of different mammals.

What has caused the different development of papillary patterns upon the various fingers? In this paper this question will be discussed only in passing: for a definite answer further investigations are needed, especially applied to material collected for this special purpose.

Fully acknowledging the difficulties entailed by the complications mentioned, and also the uncertainty which attaches to my conclusions, I have found this topic contains so many problems of special as well as of general interest that I venture to publish my results, hoping that they may be considered, not as giving definite answers to the many questions raised, but as a sufficient basis for further investigations.

CHAPTER I.

(*a*) Historical Remarks.

Our modern knowledge about the patterns formed by the papillary ridges on human fingers is founded above all upon the results of Galton, given in a series of papers among which his book on *Finger Prints* (1892) holds the first rank. A voluminous literature, from many different countries, has, however, preceded as well as followed the publications of Galton. A great part of modern literature deals with the practical use of finger-prints as means of identification (e.g. Daae (1904), Henry (1901), Windt u. Kodiczek (1904)), while among older publications those of Purkinje (1823) and of Alix (1868) should be mentioned especially as giving a general introduction to the various questions involving the study of papillary patterns. The papers of Kollmann (1883–85), of Blaschko

(1884–97) and of Klaatsch (1887–88), constitute introductions to the ontogeny, the histology and the phylogeny of papillary ridges respectively.

Of special interest to the last-named side of the question are also two very valuable papers by Whipple (1904) and by Schlaginhaufen (1905 *a*) treating the papillary patterns, the former of the palms and the latter of the soles of mammals, both showing the homology between the papillary ridges of man and the ridges on the pads of different mammals, the whole arrangement being especially similar in marsupials, primates and man. Each palm and sole of the animals mentioned shows 11 pads, viz. five apical pads at the distal end of fingers and toes, four interdigital

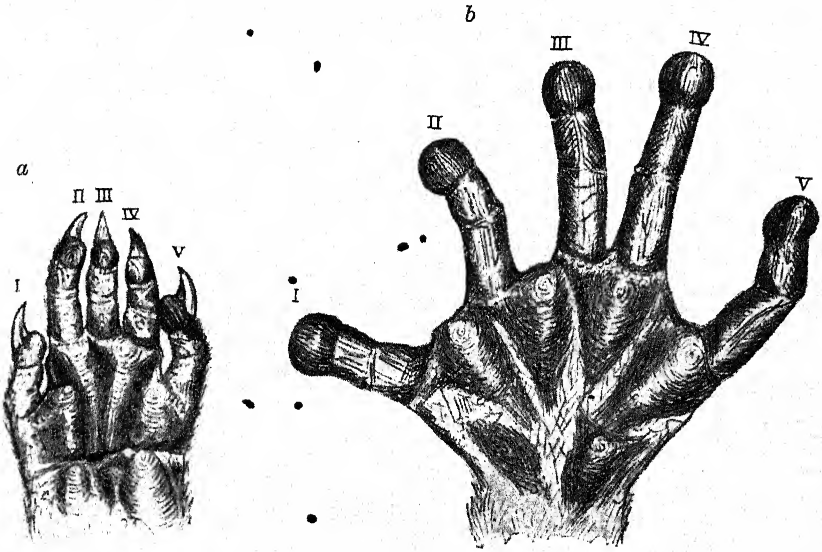


Fig. 1 *a*. *Didelphys marsupialis*, left anterior chiridium. (Whipple, 1904, Fig. 9, p. 279.)
b. *Galago demidoffi*, left anterior chiridium. (Whipple, 1904, Fig. 12, p. 283.)

between the bases of the latter, and two more proximal ones, "thenar" below the base of the first finger (toe) and "hypothenar" at the ulnar side of palms and soles.

In the hands and feet of man papillary patterns may in rare cases be found at the same 11 places, although these patterns are undergoing a reduction process, so that very often the more distal patterns only, and especially the apical ones, are present. Both authors have also, quite independently, demonstrated in lower mammals a development of the papillary ridges from small epidermal warts, each carrying the opening of a sweat gland.

With regard to the different types of papillary patterns Whipple (1904) maintains that the typical pattern of elevated pads is that of a "whorl" in which the papillary ridges are arranged concentrically round the highest point of the pad. When the pads are flattened, as is the case both with the higher apes and with man, this original pattern is reduced to more simple types.

Schlaginhaufen (1905 *b*), agreeing with the view of Whipple, gives further proof, not only of the reduction of the pattern in higher primates, but also of its gradual development in the lower ones. This is shown especially in the apical patterns of the sole.

Also Wilder has in a series of papers (1897–1919) treated the special configuration of papillary patterns as found on the human palms and soles, these patterns representing a continuous series of reduction stages from those of the elevated pads. The apical patterns of fingers and toes of degenerated or psychically abnormal individuals have finally been thoroughly investigated especially by d'Abundo (1891–1894), by Féré (1891–1906) and by Cevidalli (1906–11).

Lists of literature are given by Schlaginhaufen (1905 *b*) and later especially by Wilder (1916). But even after that time, and besides the papers mentioned in the lists, important contributions to the discussion of papillary patterns have been given by Kleiweg de Zwaan (1911, 1914), Collins (1913), by Furuse (1913), Poll (1914–22), by Kubo (1918), Hasebe (1918), Stockis (1921, 1922) and others.

The contents of these papers will partly be taken into consideration in the following chapters.

(*b*) Indications of Heredity of Papillary Patterns.

Galton has in his famous book on *Finger Prints* (1892) discussed the question of heredity in a chapter containing much valuable material. Through a statistical treatment of the finger-patterns of 150 fraternal couplets; further, through an investigation of 17 sets of twins, and finally also through a comparison of children with their parents in cases in which both parents were "like-patterned," Galton reached a conclusion expressed in the following words (p. 189): "The decided tendency to hereditary transmission cannot be gainsaid in the face of these results, but the number of cases is too few to justify quantitative conclusions."

More conclusive evidence is given by Wilder (1902, 1904, 1908, 1916, 1919), although his attention has been directed more to palm and sole patterns than to those of the fingers. About 50 sets of twins have been investigated by him with the result that hands and feet of duplicate

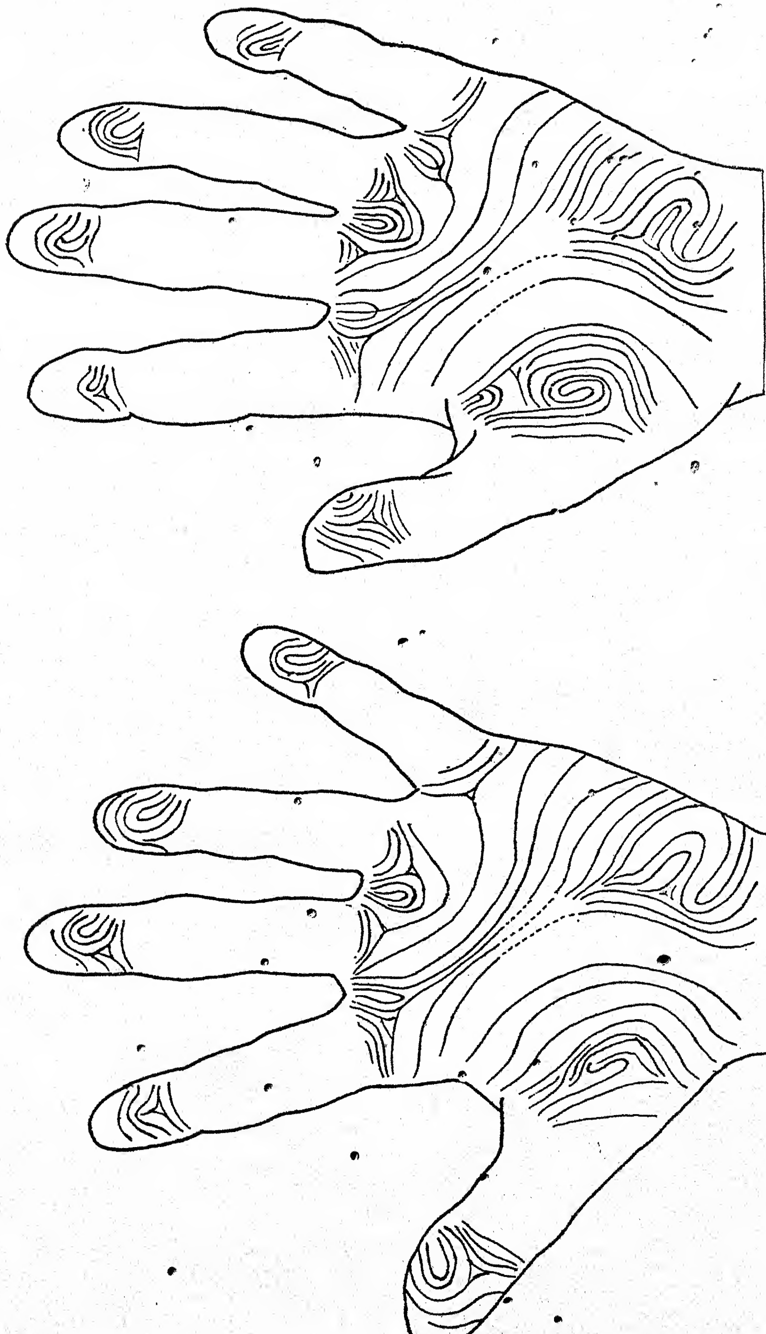


Fig. 2. Palm prints of the *M*-twins (males). Right hands. (Wilder, 1919, Fig. 16.)

(identical) twins are found to be strikingly alike with regard to the occurrence of patterns upon palms and soles, and also in their general type, while this similarity (1919, p. 411) "does not extend in the least to the finer details, the 'minutiae' of Galton." Examples are given of twins, in the palms of which the 11 original patterns (five apical, four interdigital, one thenar and one hypothenar) are all present (Fig. 2).

Considering the very rare occurrence of such cases (according to Wilder one or two among more than 1200 single individuals) their occurrence in a pair of identical twins shows that the development of patterns is determined in the egg, and therefore also that it most probably will be inheritable.

Wilder has also (1916) given the results of investigations of whole families, in one of which the father had hands with both thenar and hypothenar patterns, while these patterns were wanting in the hands of the mother. In the hands of six children "hypothenar" did not occur at all, while the thenar was present in no less than ten hands. The author concludes (p. 232): "As the thenar pattern is usually so rare (*ca.* 4 per cent.) its almost universal occurrence in this family is without doubt due to direct inheritance from the father" and further (p. 233): "Except for the failure—in two of the 12 cases, the character acts like a Mendelian dominant. On this basis the failure in these two cases may be explained by (1) that the father himself is heterozygous, or (2) that the character is not a unit character."

As already mentioned, Wilder does not seem to have given special attention to the apical patterns, the "finger-patterns"; here, therefore, the heredity cannot yet be considered proved, and still less so their special mode of inheritance, even if the statistics of Galton as well as the analogy with the just-mentioned patterns of palms and soles both represent strong evidence in favour of heredity.

In the material of finger-prints belonging to the Court of Justice of Kristiania there exist also several examples of a very conspicuous similarity between the prints of two, or even of three brothers. Especially in one case in which a very rare formula of finger-prints ("arches" on all ten fingers) occurs in two brothers the indication of heredity is very strong.

Before this question can be definitely solved it will be necessary to settle a series of other questions as to the statistical occurrence of the different patterns upon each of the fingers, the correspondence between different fingers, and the symmetry between the fingers of the right and left hands in respect of pattern.

Such knowledge about these facts is indispensable for a sound criticism of the family histories.

CHAPTER 2.

General Statistics of Finger-Prints.

As early as 1823 Purkinje showed that the finger-patterns represent a series of well-definable types. Modern terminology is however, above all, based upon the fundamental works of Galton, distinguishing three main types of papillary patterns, viz. whorls, loops, and arches (Fig. 3).

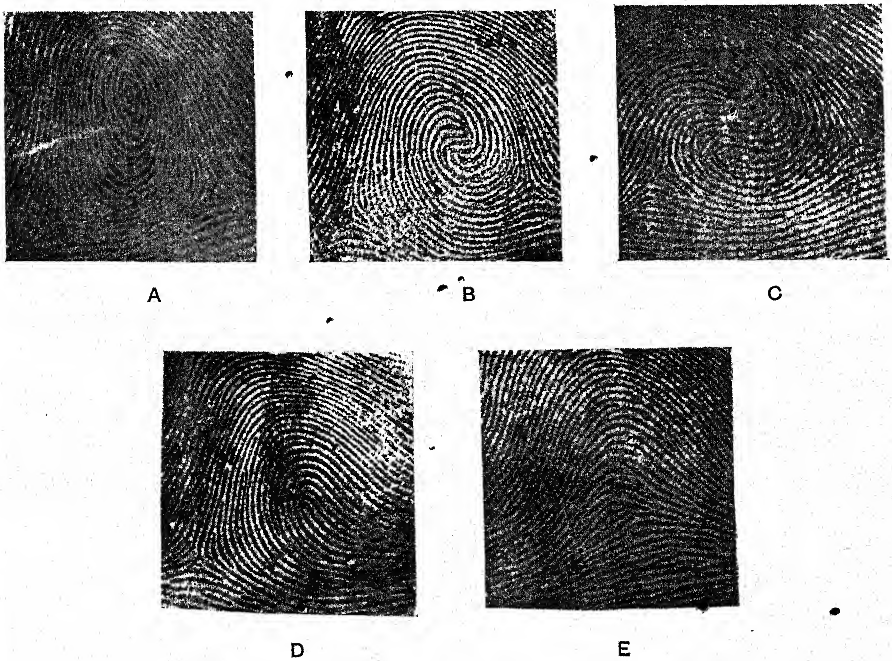


Fig. 3. Types of finger-patterns. *A–C*, whorls (*A*, typical whorl; *B*, double spiral; *C*, double (twinned) loop); *D*, loop; *E*, arch.

The whorls are characterised by the existence of two deltas, that is, on each side of the pattern one ridge dichotomously divided or two parallel ridges dichotomously separated, thus forming a triradius and embracing the central part of the pattern. In this part the ridges may be circular, form single or double spirals or even other more irregular figures.

In the loops there is only one delta, while one or more ridges form loops opening towards the side of the finger opposite to that of the delta.

The loops may open towards the radial or towards the ulnar side of each finger and according to this they are called radial or ulnar loops.

The arches represent the simplest patterns, the ridges here running in more or less deep curves from side to side of the finger without making any backward turn or twist. There is no real delta in the arch or, if a delta should exist, there is no ridge between this delta and the top ("core") of the loop-axis.

Between these three types there exist many transitions; at times, therefore, it may be difficult to distinguish the types. But, for the identification of criminals, the experts have in such cases agreed to use for their classification a certain scheme which is explained and richly illustrated, among others, by Henry (1901), and by Windt u. Kodiczek (1904).

A statistical treatment of finger-patterns was undertaken first by Galton (1892), arranging the prints of 500 individuals according to the above characterised types. Similar statistics have been published also by later authors, their material consisting of normal or of degenerate individuals belonging to different human races. A comparison of the results of the statistics published shows differences between them on essential points, and it seemed necessary, in order to have a safe basis for further consideration, first of all to make up new general statistics built upon a material large enough to exclude all disturbing effects of chance.

I have, therefore, with gratitude, made use of the opportunity offered to me by the Director of the Office of Identification in Kristiania, Mr Waldemar Hansen, of studying the large material of finger-prints in his office, taken from a number of 24,518 individuals and counting, therefore, ten times this number of fingers[1]. The costs of a revision of this material have been provided by the Nansen Fund, and the extensive and tiresome statistical treatment of it has been carried out by Miss Marit Lien. I wish to use this opportunity of expressing my deep gratitude for the very valuable support, in these ways, given to my investigation.

Table I gives a general view of the way in which the different types of finger-patterns are distributed on the fingers, while the figures added in [ ] give the results of Galton (1892) derived from his material of 500 individuals.

It is seen from the first horizontal line of this table that the three types of finger-patterns are very unlike with regard to their numerical

[1] A preliminary account of the main results of this investigation has been given by me in 1923 (*a*).

appearance within the whole material (245,180 fingers), the whorls (62,883) appearing in a percentage of 25·65, the loops (164,150) in 66·95 per cent., while the percentage of arches (18,147) is only 7·4. Such a difference at once indicates that the finger-patterns in their occurrence will prove to be subject to some constitutional law.

The results of Galton, values of respectively 26 per cent., 67·5 per cent. and 6·5 per cent., agree upon the whole very well with those just mentioned from the Norwegian material. The slight differences found, also with regard to the various fingers, may be due either to racial differences between the two populations investigated, or to the fact that the material of Galton was considerably less extensive than that used for Table I.

In Table I we find, further, a conspicuous difference in the occurrence of radial and ulnar loops, the latter appearing in a percentage of 61·14 of the number of fingers, while the percentage of radial loops is only 5·81.

The above statistics refer to the whole material of fingers taken together. The picture here given will be very much heightened through a consideration also of each finger separately. All statistical data concerning digits I–V will be found in separate lines of Table I.

Digit I shows a percentage of whorls (35·04 per cent.) far beyond that of the average, and it is further seen that this surplus is especially due to the very frequent occurrence of whorls on the first finger of right hands (41·66 per cent.). In contrast both loops and arches give values below the average, the lowest being that of radial loops occurring only on 0·34 per cent. of first fingers.

Digit II gives a statistical picture very different from that of the first, the most characteristic features of which are, (1) the great correspondence between right and left hands, (2) the surprisingly high value of radial loops (23·98 per cent.) and the very high value also of arches (16·47 per cent.).

The occurrence of whorls upon digit II is somewhat, but not much, higher than the average, while ulnar loops (30·66 per cent.) compared with all other fingers are very much reduced in their numerical frequency.

Digit III is characterised first of all through a great surplus of ulnar loops (70·44 per cent.), while high values are found also for arches (11·03 per cent.). Whorls, on the other hand, and radial loops show low values. As in digit II there is a good correspondence between right and left hands.

In digit IV we meet with characteristics very similar to those of

Fingers	Hands	Whorls	Loops rad.	Loops uln.	Loops sum total	Arches	
		% of fingers. (245180)					
All	both	25,65 [26]	5,81	61,14	66,95 [67,5]	7,40 [6,5]	100,00
	right	29,38	5,94	57,76	63,70	6,42	100,00
	left	21,92	5,68	64,52	70,20	7,88	100,00
1st	both	35,04	0,34	60,71	61,05	3,91	100,00
	right	41,66 [44]	0,36	55,37	55,73 [53]	2,61 [3]	100,00
	left	[30] 28,42	0,31	66,05	[65] 66,36	[5] 5,22	100,00
2nd	both	28,89	23,98	30,66	54,64	16,47	100,00
	right	29,67 [30]	25,73	27,51	53,24 [53]	17,09 [17]	100,00
	left	[28] 28,10	22,24	33,81	[55] 56,05	[17] 15,85	100,00
3rd	both	16,22	2,31	70,44	72,75	11,03	100,00
	right	16,88 [15]	2,22	70,91	73,13 [78]	9,99 [7]	100,00
	left	[16] 15,55	2,40	69,98	[76] 72,38	[8] 12,07	100,00
4th	both	37,10	0,78	58,71	59,49	3,41	100,00
	right	44,98 [45]	1,21	50,74	51,95 [53]	3,07 [2]	100,00
	left	[31] 29,22	0,35	66,68	[66] 67,03	[3] 3,75	100,00
5th	both	11,01	1,64	85,18	86,82	2,17	100,00
	right	13,72 [13]	0,17	84,26	84,43 [86]	1,85 [1]	100,00
	left	[8] 8,30	3,10	86,10	[90] 89,20	[2] 2,50	100,00

TABLE I. Pattern-types of 1st—5th fingers in percentage of the number of fingers.

digit I. The whorls here again appear in a percentage (37·10) very remarkably surpassing the average value, this surplus being, as in digit I, especially due to the very frequent occurrence of whorls upon digit IV of right hands (44·98 per cent.). The similarity with the first finger holds good also for the statistical occurrence of loops and arches.

Digit V finally is, still more so than digit III, characterised through a very high percentage of ulnar loops (85·18 per cent.), while all other types are on the minus side of the average values. In the occurrence of whorls upon digit V there is a marked difference between right (13·72 per cent.) and left hands (8·30 per cent.).

Interesting supplementary evidence as to the characteristics of the various fingers, now studied on Table I, is found in the statistical distribution of each pattern-type as shown in Table II (p. 12).

With regard to the whorls Table II shows that this type is on all fingers more frequent in right than in left hands. There is also a very characteristic difference between the percentage of whorls upon the various fingers. Remembering that an equal distribution of any type should give for each finger the average value of 10 per cent., we find this value far surpassed in digits I and IV of right hands with 16·24 per cent. and 17·53 per cent. respectively, while the percentages of whorls on digits III and V are seen to be very low.

With regard to the loops the interest lies first of all in a consideration of the radial ones, these being, as already mentioned, very particular in their distribution. Radial loops occur, as will be seen, with no less than 82·57 per cent. of their whole number upon second fingers only, a little more than half of this value (44·29 per cent.) falling on right hands. On all other fingers, especially on digits I and IV, radial loops are very rare. In digit V there is a marked difference between right and left hands with regard to the statistical occurrence of radial loops, their values being here 5·33 per cent. in left hands, and only 0·29 per cent. in rights.

The numerical appearance of ulnar loops is of less interest in so far as it seems to be only a function of that of other pattern-types, the ulnar loop being, as a fundamental type, always present where other more special patterns have not taken its place.

The arches have, like the radial loops, their highest values on digit II (44·50 per cent.), somewhat more on right than on left hands. Also on digit III arches are relatively frequent (29·81 per cent.), but here as well as on the other fingers more arches are found on left hands than on rights.

Finger-pattern				% of the type												
				All fingers		1st finger		2nd finger		3rd finger		4th finger		5th finger		
Type		number	% of fingers	right	left	right	left	right	left	right	left	right	left	right	left	
Whorls		62883	25,65	57,27 %	42,73 %	16,24 %	11,08 %	11,57 %	10,96 %	6,58 %	6,06 %	17,53 %	11,39 %	5,35 %	3,24 %	100,00
				100 %		27,32 %		22,53 %		12,64 %		28,93 %		8,58 %		100,00
Loops	rad.	14244	5,81	51,10	48,9	0,62	0,53	44,29	38,28	3,82	4,14	2,08	0,62	0,29	5,33	100,00
				100		1,15		82,57		7,96		2,70		5,62		100,00
	uln.	149906	61,14	47,24	52,76	9,06	10,80	4,50	5,53	11,60	11,45	8,30	10,90	13,78	14,08	100,00
				100		19,86		10,03		23,05		19,20		27,86		100,00
	Sum total	164150	66,95	47,57	52,43	8,32	9,92	7,96	8,37	10,92	10,81	7,76	10,01	12,61	13,32	100,00
				100		18,24		16,33		21,73		17,77		25,93		100,00
Arches		18147	7,40	46,77	53,23	3,53	7,05	23,09	21,41	13,50	16,31	4,15	5,08	2,50	3,38	100,00
				100		10,58		44,50		29,81		9,23		5,88		100,00
		245180	100,00													

TABLE II. Distribution of patterns upon different fingers in percentage of the type.

Summing up the statistical results we find very peculiar characteristics of each of the ten fingers.

Digits I and IV form a group characterised by *high percentages of whorls* and by a very considerable *difference in their occurrence between right and left hands.*

Digit II differs from all other fingers in the *very frequent occurrence of radial loops and also of arches,* instead of ulnar loops. Characteristic of this finger together with digit III is also the relatively *great statistical correspondence between right and left hands.*

Digits III and V have the greatest number of ulnar loops, while arches are more frequent on the third finger. Digit V shows, like digits I and IV, a considerable statistical difference between right and left hands.

The figures of Galton (added to those of Table I) prove to be in the main lines consistent with my results, even if there are some differences in details. The most remarkable difference is that of the whorls on digit I showing, according to Galton's results, 44 and 30 per cent. on right and left hands respectively, while in my material the corresponding values are 41·66 per cent. and 28·42 per cent. This difference will, together with the results also of other authors, be discussed in a following chapter.

Appendix to General Statistics.

Before leaving the statistics of pattern-types a few other questions, first raised by Galton, must be mentioned.

The statistical rate of *symmetry between the fingers of both hands* is shown in Table III for all fingers at a time in the last horizontal row, and for each of the five fingers in the upper rows. Galton's figures are added in ( ).

The highest rate of correspondence between right and left hands is that of digit V, amounting to 87·61 per cent. of all individuals investigated; but more than 80 per cent. are here seen to be due to cases of ulnar loops and therefore are of no great interest. Galton has, for this reason, omitted the fifth finger in his comparison. In digit III also the great percentage of cases of symmetry (73·83 per cent.) is to a very high degree due to the ulnar loops (57·76 per cent.). High rates of symmetry are, however, found also in digits I and IV, 74·05 per cent. and 71·91 per cent. respectively; and here not only the ulnar loops but also the whorls play a prominent part in the statistical picture of symmetry with 23·93 per cent. and 24·72 per cent. respectively. The lowest per-

centage of symmetry is found for digit II, 51·28 per cent. only of all individuals having here the same pattern-type on both hands.

No other finger has all different pattern-types so equally represented statistically as digit II; this finger, therefore, gives better than any of the others material for a comparison of the various patterns with regard to their symmetrical occurrence.

Fingers of right and left hand.	Whorls	Loops			Arches	Total
		rad.	uln.	Total		
1st finger	23,93 (24)	0,02	48,2	48,21 (48)	1,9 (2)	74,05 (74)
2nd "	18,9 (20)	9,27	14,96	24,34 (38)	8,14 (9)	51,28 (67)
3rd "	10,10 (9)	0,20	57,76	57,96 (65)	5,76 (3)	73,83 (77)
4th "	24,72 (26)	0,07	45,40	45,47 (46)	1,72 (2)	71,91 (74)
5th "	6,01	0,004	80,44	80,45	1,15	87,61
All	1,51	0	4,29	4,29	0,18	5,99

TABLE III. Correspondence between fingers of right and left hands. Percentage of 24,518 individuals. Galton's results added in ( )

2nd finger	Whorls	Loops		Arches
		rad.	uln.	
Occurrence of type in % of fingers	28,89 %	23,98 %	30,66 %	16,47 %
Symmetry of type in % of all cases of Symmetry.	36,86 %	18,08 %	29,17 %	15,87 %

TABLE III A. Comparison of pattern-types as to their symmetrical occurrence.

Taking all cases of symmetry in the patterns of second fingers as a whole, it will be found that symmetry of whorls occurs in 36·86 per cent. of these cases, of radial loops in 18·08 per cent., of ulnar loops in 29·17 per cent. and of arches in 15·87 per cent. A comparison of these figures with the percentage given in Table I, showing the general distribution of patterns on digit II, proves (Table III A) that whorls play a considerably more prominent part within the cases of symmetry (36·86 per cent.) than in the general distribution of patterns in the whole material (28·89

per cent.), while all other pattern-types show a percentage of symmetry lower than that of their general occurrence.

A similar result was reached also by Galton (1892, p. 129) proving the "relationship" between whorls, on a centesimal scale, to be considerably greater than that of the loops.

Before leaving Table III, a few words should be said with regard to the statistical results of Galton added in ( ). As in Table I his figures agree with mine in the main lines, but here one exception must be mentioned, viz. the great difference in our figures with regard to the loops of digit II, 38 per cent. (Galton) to 24·34 per cent. in my results, this difference influencing of course also the sum total for this finger (67 per cent.—51·28 per cent.). Such a difference, however, is easily explained as a consequence of Galton's treating all loops together as one group, while in my tables ulnar and radial loops are separated. Besides the cases of symmetry within each of these groups considered by me, Galton has counted also those cases in which one hand has an ulnar loop while there is a radial loop on the other side.

In Table IV, again, a question is treated also raised by Galton (1892, p. 121) about "the close similarity between corresponding entries relating to the same and to the opposite hands."

After having demonstrated the figures found in ( ) in Table IV of this paper, Galton adds (p. 122):

"Though the unanimity of the results is wonderful, they are fairly arrived at and leave no doubt that the relationship of any one particular digit...to any other particular digit is the same, whether the digits are on the same or on opposite hands."

A statistical correspondence like that here shown by Galton would, indeed, at first glance seem a very strange feature, and one which ought to be taken into consideration in any discussion about the constitutional nature of finger-patterns. It therefore seemed necessary for me to test the statistical results of Galton upon the larger material at my disposal (Table IV).

With regard to the mere figures my results confirm those of Galton, even if the percentages reached are not exactly the same, and if for the loops, especially those of the second finger, the same difference is found as in Table III, radial and ulnar loops not being separated in Galton's material.

But an attentive consideration of each special figure has made me look upon the conformity between couplets of fingers of the same and of opposite hands as a mere consequence of the general distribution of

Fing.	Whorls		Loops				Arches		Total	
			rad.		uln.					
	Hand same	Hand opposite	Hand same	Hand opposite	Hand same	Hand opposite	Hand same	Hand opposite	Hand same	Hand opposite
I and II	16,92 (16)	16,72 (15)	0,07	0,05	22,43 (35)	20,74 (33)	2,14 (2)	2,12 (2)	41,56 (53)	39,63 (50)
I " III	10,22 (9)	9,97 (8)	0,02	0,01	46,48 (48)	45,13 (47)	1,14 (1)	1,64 (1)	57,86 (58)	56,74 (56)
I " IV	19,58 (20)	17,01 (18)	0,004	0,004	41,45 (40)	38,26 (38)	0,79 (1)	0,78 (1)	61,82 (61)	56,06 (57)
I " V	7,06	6,22	0	∂	56,70	54,81	0,69	0,57	63,84	61,60
Means	13,45	12,48	0,024	0,016	41,62	39,76	1.19	1.28	56,18	53,51

TABLE IV. Correspondence between different fingers of same and opposite hands (percentage of 49,036 hands). Galton's results from 500 individuals are added in ( ).

finger-patterns, depending above all upon the statistical correspondence of *second* as well as of *third* fingers of both hands. As soon as one of these two fingers is used for the comparison, a result like that reached by Galton will be obtained, the asymmetry of the other link of comparison making its effect in the percentage of the "same" hand to the same degree as in that of the "opposite." In a comparison between digit I and digit IV, in both of which the correspondence between right and left side is less pronounced, the difference between "same" and "opposite" hand is seen to be rather considerable, the sum total here giving for the "same" hand 61·82 per cent. (Galton 61 per cent.) while for the "opposite" it is only 56·06 per cent. (Galton 57 per cent.). The same is found not only in the sum totals but also in each special figure of Table IV: if in one case (for example the ulnar loops of digits I and III, the radial loops of digits I and IV, the arches of digits I and IV) the percentage of correspondence is found to be equal for the "same" and the "opposite" hands, it is always also found (Table I) that one of the two links of comparison shows a more or less complete statistical symmetry with regard to the pattern in question.

CHAPTER 3.

DISCUSSION OF THE STATISTICAL OCCURRENCE OF FINGER-PATTERNS.

Many questions may arise from an attentive consideration of the statistical results just studied. Above all, however, answers are wanted to the following two groups of questions. What are the reasons for

(1) The peculiarities of digits I and IV—their statistical similarity, their great frequency of whorls and the very considerable surplus of this pattern upon *right* hands—the last-named question applying also to digit V?

(2) The peculiarities of digit II, viz. the surprisingly high percentage of radial loops, with the very high value also of the percentage of arches, the last-named characteristics being to a certain degree found also in digit III?

The answers to these questions can certainly not yet be given, and even a thorough discussion of them would be outside the scope of this paper. Some understanding of the characteristics of each separate finger will, however, be of importance for our discussion of the heredity of papillary patterns; it will therefore be necessary to state in a few words the different ideas which may present themselves for an explanation of the statistical peculiarities mentioned.

First, however, the question should be answered whether the material used by me for the above statistics may be considered as representative.

No objection can be raised against the size of a material containing 24,518 individuals; but the material is selected in so far as it consists mainly of criminals while, on the other hand, it represents a mixture of the several races composing the Norwegian population. My results have been compared and agree very well with those of Galton from 500 persons; but he does not say from whence this material was taken, and it may therefore perhaps also consist of criminals.

For this reason I have thought it important to undertake a thorough comparison with other statistics available from literature, especially with the statistical results from other human races found in the papers of Schlaginhaufen (1906) for a group of artists from India, Gasti (1907) and Falco (1908) for various groups of the Italian population, Kleiweg de Zwaan (1911) for 500 natives from Sumatra and 1300 from Nias, Furuse (1913) and Kubo (1918) for a great number of criminals from different parts of Japan and Korea, and Hasebe (1918) for school children, students and nurses from Nigata (Japan) and for the Aino people. If, on comparison with all these statistics, my results upon the Norwegian material should prove wholly or partly to be confirmed, then I think we shall be right in considering the peculiarities in question as general characteristics of the apical patterns of human hands.

Such a comparison is carried out in Tables V–X, the contents of which will now be considered.

Table V gives for the populations above-mentioned the total occurrence (in percentage of fingers) of each pattern, the radial and ulnar loops not being, however, treated separately in the papers of Galton and of Kleiweg de Zwaan. The table shows that, in all cases, the loops represent the most frequent occurrence (*ca.* 51–67 per cent.), while the arches are relatively very rare (1·6–7·4 per cent.). All populations investigated agree also with regard to the relative occurrence of radial and ulnar loops, the frequency of the latter amounting to more, and often considerably more, than ten times that of the former. The percentages of whorls give an interesting picture in so far as this pattern-type in its occurrence seems to show characteristic racial differences. In the populations from Eastern Asia we find no great difference between the percentage of whorls (*ca.* 43–45 per cent.) and that of ulnar loops (*ca.* 48–50 per cent.), while in the English and Norwegian populations this difference is very great, the percentage of whorls being less than one-half of that of the ulnar loops (Norwegians: 25·6–61·1 per cent.). The

populations from India, Nias and the Aino people, as well as those from Italy represent a medium relation between whorls (32–39 per cent.) and ulnar loops (53–61 per cent.).

Races		Whorls	Loops Rad	Loops Uln	Loops Total	Arches	Indiv. investigated		Author
Korea		45,18	3,15	48,71	51,86	2,62	700	Criminals	Kubo 1918
Japan	Eitoho	45,70	3,43	48,60	52,03	1,90	300	"	" "
	Ischigaya	45,16	3,84	48,92	52,76	1,81	700	"	" "
	Sugano	45,18	4,2	47,65	51,85	2,62	1528	"	Furuse 1913
	Nigata	43,6	3,2	50,4	53,6	2,8	276	Students Nurses	Hasebe 1918
Sumatra		45.14			53,13	1,72	500	Natives	Kl. de Zwaan 1911
India		36,1	2,7	59,2	61,9	1,6	27	Artists	Schlaginhaufen 1906
Nias		34,73			62,88	2,39	1300	Natives	Kl. de Zwaan 1911
Aino		31,8	3,8	61,4	65,2	2,9	55	Children	Hasebe 1918
Italy		36,46	4,44	54,00	58,44	4,72	1579	Criminals	Falco 1908
Italy		39,0	3,9	53,0	56,90	4,7	100	Normal	Gasti 1907
"		39,3	3,7	53,7	57,40	3,7	100	Criminals	
" (German race)		29,2	5,1	57,9	63,0	7,4	100	„Stranieri"	
England		26,00			67,3	6,5	500	"	Galton 1892
Norway		25,65	5,81	61,14	66,95	7,40	24518	Criminals	Bonnevie 1922

TABLE V. Statistical occurrence of pattern-types in different human races.

China	38,7			57,1	4,2	5000	Brachycephals	Collins 1913
India	36			61	3	2000	Brachycephals	
"	30,5			65	4,5		Dolichocephals	
England	20,15			74,85	5	5000	Dolichocephals	

TABLE V A. Statistics of pattern-types, combined by Collins (1913) with the occurrence of Brachy- and Dolichocephals.

The results of Collins (1913) from Chinese, Indian and English populations, shown in Table V A, give a welcome supplement to the abovementioned. The Chinese here come in between the Japanese and Indians with regard to the statistics of their finger-patterns. The difference of

Collins' result from those of Galton with regard to English populations is, however, very notable.

The distribution of each pattern in the various fingers is shown in Tables VI–IX, these tables taking, however, only the larger populations in consideration. The distribution of whorls is seen from Table VI. It proves for each of the populations investigated to be characterised by the same peculiarities found in the statistical results of Norwegians alone, viz. a relatively very frequent occurrence of whorls upon digits I and IV and especially upon these fingers of right hands, while the lowest amount of whorls is found on digits III and V, the statistical difference between right and left hands being conspicuous also with regard to digit V.

Dig.		I		II		III		IV		V		
Hands		r	l	r	l	r	l	r	l	r	l	
Korea ♂		64,6	54,4	43,4	40,8	33,8	35,0	63,4	56,8	32,0	22,8	44,7
" ♀		61,5	56,5	47.5	47,5	33,5	45,5	60,0	57,5	22,5	24,5	45,65
Japan	Ischigaya	61,1	48,8	45,0	43,2	34,0	34,8	66,1	57,9	35,2	25,5	45,16
	Sugano	57,3	49,7	47,2	40,4	33,3	37,8	66,2	58,1	36,0	25,8	45,18
Sumatra		63,3	52,5	48,3	45,7	30,6	31,0	65,0	54,0	35,2	25,9	45,14
Nias		46,6	38,1	42,75	40,7	23,4	25,6	49,3	40,3	24,0	16,5	34,73
Italy		56,46	43,68	41,52	38,23	22,27	25,16	56,90	42,79	22,66	17,71	36,46
England		44,0	30,0	30,0	28,0	15,0	16,0	45,0	31,0	13,0	8,0	26,00
Norway		41,66	28,42	29,67	28,10	16,85	15,55	44,98	29,22	13,72	8,30	25,65

TABLE VI. Whorls in percentage of fingers in the various human races.

One remark should, however, be made with regard to the two first lines of this table:

In Korea men and women have, by Kubo, been investigated separately, and it is worth notice, that in the Korean women the surplus of whorls upon the fingers of right hands is very considerably smaller than in any other population investigated, and even that on digits III and V the statistical relation between right and left hands is, with regard to the occurrence of whorls, reversed. A question to be solved through future investigations is, whether this peculiarity of the Korean women is characteristic of this population alone, or whether there may exist a general statistical difference between men and women with regard to the

distribution of whorls. I have upon a family material of about 180 persons examined this question with a negative result, no characteristic statistical difference here being found between men and women. This material is, however, too small to justify general conclusions.

The distribution of arches upon the various fingers is shown in Table VII. Also here we find in each one of the populations the same characteristics emphasised above, viz. a relatively high percentage of arches upon digit II and in part also on digit III. A remarkable feature of Table VII is the very great difference between the Asiatic races (six upper lines) and the Northern Europeans (two lower lines), the frequency of arches in the latter being raised to two or three times their

Dig.	I		II		III		IV		V		
Hands	r	l	r	l	r	l	r	l	r	l	
Korea ♂	1,4	2,2	6,2	4,4	2,2	3,0	0,8	0,8	1,0	0,8	2,28
" ♀	5,0	3,0	7,0	5,5	2,0	4,0	0,5	0,5	0	0	2,75
Japan: Ischigaya	1,1	2,2	4,2	5,6	2,1	2,3	0,2	0,3	0,1	0	1,81
Japan: Sugano	0,9	2,5	7,1	6,9	3,0	3,5	0,7	0,6	0,4	0,6	2,62
Sumatra	0,5	1,7	5,0	4,0	2,0	2,0	0,6	1,0	0,2	0,2	1,72
Nias	1,2	2,5	4,7	5,4	3,1	4,5	1,0	1,2	0,1	0,2	2,39
Italy	1,26	3,10	11,65	10,7	7,02	7,97	1,83	1,45	0,76	1,45	4,72
England	3,0	5,0	17,0	17,0	7,0	8,0	2,0	3,0	1,0	2,0	6,50
Norway	2,61	5,22	17,09	15,85	9,99	12,07	3,07	3,75	1,85	2,50	7,40

Table VII. Arches in percentage of fingers in the various human races.

amount in the former, the Italians forming a transition between both. With the exception of digit II arches are generally found to be most numerous upon left hands. Also here the Korean women show, according to Kubo, a peculiar deviation, having in their digit I of right hands a surprisingly high rate (5 per cent.) of arches.

A similar correspondence between the different races exists with regard to the loops (Table VIII), these patterns being always found very frequently on digit III and still more so upon digit V. A gradual rise of the total number of loops is found when passing from Asiatic races to the Northern Europeans. The special characteristics of the loops are

found, however, not by treating this pattern as a whole but by considering the radial and ulnar loops separately.

	Dig.	I		II		III		IV		V		
	Hands	r	l	r	l	r	l	r	l	r	l	
	Korea ♂	33,4	42,8	49,6	54,0	63,2	61,4	35,6	42,0	67,0	[illegible]	[illegible]
	" ♀	33,0	38,5	45,4	46,0	64,5	50,5	39,5	42,0	77,5	75,0	[illegible]
Japan	Ischigaya	37,8	49,0	50,4	50,7	63,5	62,6	33,7	[illegible]	64,0	73,8	52,76
	Sugano	41,4	47,8	45,4	52,4	63,3	58,4	32,3	41,2	[illegible]	72,9	51,85
	Sumatra	36,20	45,80	46,70	50,30	67,4	67,0	34,4	45,0	64,6	73,9	53,13
	Nias	52,2	59,4	52,5	53,9	73,5	69,9	49,7	58,5	75,0	83,3	62,88
	Italy	42,26	53,56	46,83	50,43	70,39	68,12	41,02	55,33	76,24	81,37	56,44
	England	53,0	65,0	53,0	53,0	78,0	76,0	53,0	66,0	[illegible]	90,0	[illegible]
	Norway	55,73	66,36	53,24	56,05	73,13	72,38	51,95	67,03	84,93	89,20	66,95

TABLE VIII. Loops in percentage of fingers in the various human races.

The results here gained are shown in Tables IX A and B. The radial loops in all races investigated are found to be characteristic practically only of the second fingers, somewhat more frequent on right hands than

	Dig.	I		II		III		IV		V		
	Hands	r	l	r	l	r	l	r	l	r	l	
	Korea ♂	1.0	0.6	16.8	11.6	2.4	2.6	1.0	0.4	0.4	0.2	3.70
	" ♀	0	2.5	7.5	13.5	0	1.5	1.0	0	0	0	2.60
Japan	Ischigaya	0.2	0.7	17.2	14.9	2.4	1.8	0.4	0.3	0.3	0.2	3.54
	Sugano	0.8	0.9	12.6	13.2	3.1	3.7	2.1	1.4	1.8	2.4	4.20
	Italy	0.37	1.13	20.0	18.4	2.27	2.40	0.63	0.19	0	0	4.44
	Norway	0.36	0.31	25.73	22.24	2.22	2.40	1.21	0.35	0.17	3.10	5.81

TABLE IX A. Radial loops in percentage of fingers.

on left ones. Here again the Korean women form an exception, having more radial loops on digit II of left hands. The difference between races with regard to the total number of radial loops is not very considerable, their percentage varying from 2·6 per cent. in Korean women to 5·8 per

cent. in the Norwegians. Since, however, practically the whole augmentation in the number of radial loops is concentrated upon digit II, the difference between this finger and the others is very much more accentuated in the last-named population than in those of Eastern Asia.

The ulnar loops (Table IX B) show, as would be expected from the distribution of the other patterns, their highest statistical values upon

Dig.		I		II		III		IV		V		
Hands		r	l	r	l	r	l	r	l	r	l	
Korea o		32,4	42,2	32,8	42,4	60.8	58.8	34.6	41.6	66,6	76.0	48.8
" o		33.0	36.0	38,0	32,5	64.5	49.0	38.5	42.0	77.5	75.0	48.60
Japan	Tochigaya	37.6	48.3	33.2	35.8	61.1	60.8	33.3	41.2	64.3	73.6	48.92
	Sugano	40.6	46.9	32.8	39.2	60.02	54.7	30.7	39.8	61.4	70.5	41.65
Italy		41.89	52.43	26.83	32.03	68.12	65.72	40.39	55.14	76.24	81.37	54.0
Norway		55.37	66.05	27.51	33.81	70.91	69.98	50.74	66.68	84.26	86.10	61.14

TABLE IX B. Ulnar loops in percentage of fingers.

digit V, where no other pattern has its special occurrence. Then comes digit III where, as we have seen, the ulnar loops have to give way for a certain amount of arches special to this finger—and further, digits IV and I on which the whorls, and digit II on which also the arches and radial loops, assume a prominent place in the statistical figures.

Summing up the results of Tables V–IX we reach the following conclusions:

There exists with regard to the frequency of each pattern-type a very conspicuous difference between different human races, but all races investigated have *with regard to the distribution of patterns upon the various fingers* certain features in common, viz. *a relatively high amount of whorls upon digits I and IV* especially those of *right* hands, *a high amount of arches upon digit II* and *to some extent also on digit III, and finally a relatively very high amount of radial loops upon digit II.*

The populations investigated being of very different origin it seems probable, therefore, that these statistical characteristics of each special finger should be considered a common characteristic of the distribution of apical patterns upon human hands. The Norwegian material of criminals used for the statistics of this paper, and showing all the characteristics just mentioned, should therefore in so far be considered as fully representative.

We now turn to the question whether satisfactory explanations have been, or may be, given for the statistical difference between the fingers with regard to the distributions of papillary patterns.

In the discussion about patterns three different views have been urged and maintained by several authors, the papillary patterns having been considered from a phylogenetic, from a physical, and from a functional point of view.

(*a*) The phylogenetic side of this question has, as already mentioned, been discussed especially by Klaatsch (1887–88), by Whipple (1904), by Schlaginhaufen (1905) and by Wilder (1916). These authors all, in full agreement, maintain the homology of papillary patterns in man with those of the elevated pads in mammals.

The occurrence of papillary patterns upon the elevated pads of palms as well as of soles has been studied especially in a series of Marsupials and Primates, but also in other mammals. A very intimate connection has been observed between pads and patterns not only with regard to the contemporaneous occurrence of both structures but also with regard to the degree of elevation of the pads and the special configuration of their patterns.

The 11 pads (two basal, four interdigital and five apical), characteristic of the typical mammalian palm and sole, all carry patterns which by Whipple are characterised as "primary." Among these patterns two groups are distinguished, viz. "typical patterns with an approximately concentric arrangement of ridges" and "modified patterns with a deviation from the typical arrangement of concentric ridges" (Whipple, 1904, p. 330).

The typical pattern of Whipple is represented by the whorl of our statistics. It is, therefore, of interest to recall the following sentences from Whipple's very important paper (p. 332):—

"The morphological significance of the typical pattern is of the utmost importance. To discuss this, two very important principles must be enunciated. First, it is obvious *that the occurrence in any form of a typical pattern in the location of a primary mammalian pad must indicate that at the time when ridges first developed in that region, the pad had the elevated form of the typical walking pad.*"

"The second principle is that *the relative constancy of occurrence of the typical pattern in a species or a group of related species, may be used as a criterion for determining the relative length of time during which various pads were retained* in their typical form."

With regard to the modified patterns Whipple maintains that their

occurrence is due to some kind of modification of the pad itself, among which reduction as well as flattening of the pad will play an important part, the former resulting in a degeneration of the triradii of the typical pattern (Fig. 4), while the latter causes a deviation of the concentric arrangement of ridges upon the pad area (Fig. 5). In both cases the whorl of the elevated pad may be modified into a loop or even into an arch.

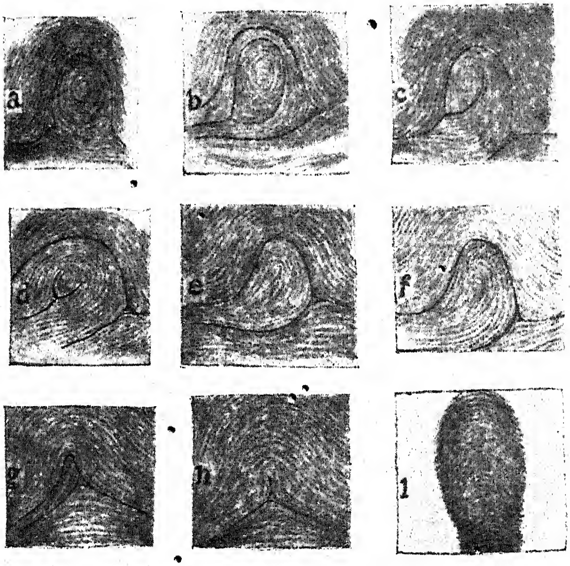


Fig. 4 *a–i*. Series of prints of human finger-tips, showing process of degeneration of pattern as a result of reduction of pad elevation: *a*, typical pattern (whorl); *f*, loop; *h*, "tented" arch; *i*, simple arch, reduction completed. (Whipple, 1904, Fig. 40, p. 339.)

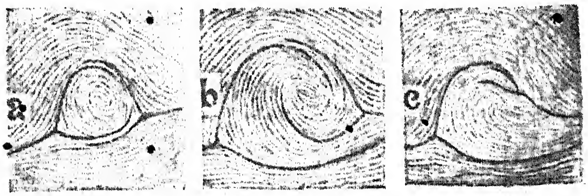


Fig. 5 *a–c*. Series of finger-patterns showing deviation from concentric arrangement as a result of a flattening of pads. (Whipple, 1904, Fig. 49, p. 351.)

Schlaginhaufen (1905 *a*, *b*), who independently had reached results very similar to those of Whipple, has, on the other hand, been able to demonstrate, on the apical patterns of Primate plantae, not only the

degeneration of patterns in higher Primates but also the gradual development of the whorl in the lower.

Thus, in lower Prosimians the apical pads of the plantae are very little elevated, and the papillary ridges are arranged as longitudinal striae surrounded by a frame of curved lines along the edge of the phalanx (Fig. 6 *a*). With elevation of the pads in higher Primates the patterns grow more complicated, the curved lines of the edge spreading in towards the centre, and the number of longitudinal striae, therefore, being reduced (Fig. 6 *b–e*). The whorls thus formed are still rather stiff, rectangular, with partly straight lines and more or less sharp angles. They were by Schlaginhaufen characterised as "Figurae tensae," and represent the Simian type of papillary patterns mentioned by Kollmann already in 1883. In the highest representatives of Primates, both apes and man, the apical pads are developed into Figurae curvatae (Schlaginhaufen) with the elegantly curved lines, so typical of the apical patterns of man (Fig. 6 *f–g*).

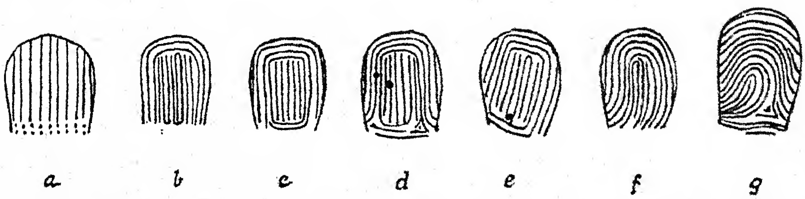


Fig. 6 *a–g*. Apical patterns of Primates. (Schlaginhaufen, 1905 *c*, Fig. 4, p. 645.)
a, Lemur; b–e, Cercopithecidae; f, Hylobates; g, Homo.

At the same time, however, the more complicated patterns, the whorls, of the elevated pads are, as described by Whipple, found to be reduced to loops and arches.

In a paper treating of the palms and soles of natives from India and Ceylon, Schlaginhaufen (1906, p. 679) remarks that human *Sinus obliqui* (loops) may perhaps have developed not only through a reduction of whorls, but also through a direct development from the Fig. tensae demonstrated in lower Primates.

The view of papillary patterns maintained by the two authors mentioned had previously been held by Forgeot (1893), and was later advocated and confirmed by Wilder (1916) in his palm and sole studies.

Féré (1891–1905), on the contrary, considers the arch as the primary type, from which the more complicated patterns have developed, the whorl representing the highest stage of development. This view was held, for the apical patterns, also by Schwalbe (1905), while for the inter-

digital patterns, as well as for the thenar and hypothenar, he agrees with Whipple (1904) in considering the whorl as the original pattern.

In spite of this theoretical discrepancy, all facts described by different authors, concerning the papillary patterns of mammals and man, seem to agree in indicating the existence of some causal connection between the pattern-type and the degree of elevation of the pad, the whorl representing the pattern of the most elevated pad.

It is in this connection of great interest to remember that, according to Johnson (1899) and Retzius (1904), human embryos, especially during their third month of development, show highly elevated apical and interdigital pads on hands as well as on feet. A close investigation of the finger-balls of such embryos might perhaps give us some clue for understanding the very characteristic statistical occurrence of pattern-types upon the various fingers. If each of the ten fingers should prove, during the embryonic period in which the papillary patterns are developed, to be characterised through a specific degree of elevation of its ball varying within a certain range, then the consequence might be also a similar regularity with regard to the statistics of finger-patterns.

Remembering the very frequent occurrence within all human races investigated of whorls upon digits I and IV, especially those of right hands, we should, according to this view, expect to find upon the fingers mentioned also some specific configuration of the embryonic balls. As will be shown later, the whorls of digit I to a great extent present the types illustrated in Fig. 5, corresponding to the broad and flattened ball of this finger. Those of digit IV, however, are practically all quite typical whorls. Their very frequent occurrence should, therefore, indicate the existence upon this finger of extraordinary high embryonic balls. It may be of interest in this connection to remember also that among Prosimians and Marsupials—the mammal groups which are supposed to be most nearly related to the human ancestors—many examples are found of a high development of the fourth finger, this finger, together with the first, being used by the climbing species for grasping round branches of trees (see Fig. 1 b of this paper). The fourth finger, further, is upon the human hand the finger which is least special in its function. It should, therefore, be supposed to show only few adaptional alterations, and to bear witness, more than any of the others, as to its historical development.

As for the preponderance of whorls upon the fingers of right hands—together with other characteristic statistical differences between the finger-patterns of both sides—it is impossible not to combine these facts with the question of right-handedness. Further investigations are

needed, however, especially of the finger-patterns of left-handed individuals, before any definite conclusion can be drawn with regard to the nature of such connection. Of great interest would be, also, any information with regard to the use of the hands by the Korean people, in which the statistics of finger-prints of right and left hands, especially those of the women, seemed upon essential points to be reversed. A characteristic difference between right and left hands has been stated also by Wilder (1916) for the papillary ridges of the palm, the most developed formula (11.9.7.5) being found "in right hands in 22–25 per cent. of the cases, while in the left hands this formula forms only 4 per cent. of the cases." Wilder here adds the suggestion (p. 236), "that this result has been gained since the adoption of right-handedness."

Before finishing this discussion of the phylogenetical view of papillary patterns, I may mention also a suggestion made by Collins (1913), that some causal connection may exist between head-shape and finger-patterns, in so far as the occurrence of whorls, "round patterns," are more frequent by Brachycephals (Chinese), while the loops as elongated patterns are more frequent in Dolichocephals, e.g. English (see Table V A of this paper). Knowing the paper of Collins only from a reference made to it by Stockis (1922) I can, of course, not enter into any discussion of his opinion, even if I must confess that it does not appeal to me as being sufficiently well founded. As already remarked by Stockis (*l.c.*), the material presented by Collins himself proves very clearly (see Table V A) that within the groups of Brachycephals (Chinese and Indians) and of Dolichocephals (Indians and English) racial differences seem to play a great part with regard to the statistics of finger-patterns. I may add also that I do not agree with Collins if he considers, in general, the whorls as round and the loops as elongated patterns. There exist, as will be shown in a following chapter, both round and elongated whorls as well as round and elongated loops (see Figs. 10–12 and Fig. 13 of this paper).

(*b*) From a physical point of view the papillary ridges have been treated by Kollmann (1883) who, basing his views upon the directions of growth in the developing epidermis, stated the existence of a lateral pressure within the epidermis itself causing its regular folding and the formation of papillary ridges. Characterising the different pattern-types he says (p. 41): "Man kann hiernach den einen Typus als denjenigen des überwiegenden Längsdruckes, den anderen als den Typus des gemischten Längs- und Querdruckes bezeichnen. Mit Bezug auf die Lagerung der Gyri dagegen ist der eine natürlich als querer, der andere als bogenförmiger Typus zu bezeichnen."

The physico-mathematical side of the question has later been treated by Kolosoff and Paukul (1906), these authors, like Kollmann, looking upon the papillary ridges as having, above all, a sensory function. The direction of papillary ridges is, according to their results, caused by the elevation of the pad itself, the ridges taking up the place of "neutral lines," that is (p. 704), "eine Reihe von Linien, welche die Richtung andeuten, in der die Leisten bei der Spannung des Hautstückes weder gedehnt noch zusammengedrückt werden."

Such neutral lines will on semi-globular surfaces form circular or spiral-shaped patterns, that is, the *whorl is the pattern typical of the most elevated pad*, the result which was reached also from the phylogenetic point of view.

The significance of such arrangement of papillary ridges in neutral lines is, by Kolosoff and Paukul, seen in an augmentation of their power of giving clear and detailed sensory impressions, all disturbing influences from the surrounding parts of the skin being excluded. "Die Leisten gleichen den auf einem weissen Papier schwarz geschriebenen Buchstaben, welche deutlicher zu lesen sind als Buchstaben auf einem beschmierten Papier" (p. 706).

(*c*) We have now reached the third point of view from which the papillary ridges have been treated, viz. that of their functional importance.

With regard to the function of papillary patterns two different theories have been maintained, the one (Whipple) considering the papillary patterns as organs of a *mechanical* use ("friction-ridges"), the other theory (Kollmann, Féré, Schlaginhaufen, Kolosoff and Paukul) looking at the papillary patterns as a *sensory* apparatus. Both theories agree, however, in the conclusion that the function of papillary patterns is best fulfilled when the direction of their ridges is at right angles to the force working against it.

Whipple (1904, p. 327), maintaining "that the function of ridges is primarily to increase resistance between contact surfaces," says further that, "the direction of ridges is at right angles with the force that tends to produce slipping, or to the resultant of such forces when these forces vary in direction."

Schlaginhaufen (1905 *a*), on the other hand, characterises the papillary ridges as Figurae tactiles, which function as (p. 615) "Hilfsorgane beim Gehen und anderen langsam ausgeführten Extremitätenfunktionen." From experiments made according to the method of Weber, he maintains that the sensory effect of papillary ridges is greatest when they are

running at right angles to the direction of pressure against the object to be touched, and further also that two parallel ridges give a greater effect if belonging to one and the same loop than if they are separate from each other (Fig. 7).

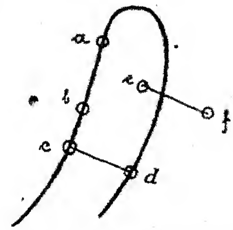


Fig. 7. (Schlaginhaufen, 1905 *a*, s. 670, Fig. 76.) Illustration of physiological experiments. Two points are distinguished more easily, when placed at right angles to the course of papillary ridges, than when parallel to them (*a–b*). The doubleness is, further, more easily distinguished when both points touch ridges forming the two arms of one and the same loop (*c–d*), than when the ridges touched are not connected with each other (*e–f*).

Looking at the human hand we should expect to find a functional adaptation above all upon digit II, this finger being of a use more varied and extensive than any other finger. And indeed, the special characteristics, mentioned above, of this finger may all be looked upon from this functional point of view, and as connected with the fact that upon the second finger not only the front of the finger-ball but also its radial side shares in its sensory function.

Remembering the position of the second finger when working alone in opposition to the first one, it seems evident that the radial side of digit II and its papillary pattern should be of great importance whether the function of those lines be of a mechanical or of a sensory nature. Among the different pattern-types, therefore, the ulnar loop will be the one least useful, its ridges running away from the radial side of the finger. Whorls and arches, the peripheral ridges of which patterns run out parallel on both sides of the finger, seem here to be of equal use as compared with each other. But no other pattern would, for the special use of the second finger, serve better than the radial loops, the ridges on the radial side of the finger here being combined into pairs as arms of one and the same loop.

This consideration of the functional importance of different papillary patterns agrees exceedingly well with their statistical distribution upon the second finger. The number of ulnar loops is here very considerably lower than upon any other finger, making in the Norwegian material

(Table I) only 30·66 per cent. of the number of fingers while 58·71 per cent. (digit IV) is the lowest value found on other fingers. The whorls give values not far above the average while arches and especially also radial loops are represented in extraordinarily high numbers, 44·5 per cent. of all arches and 82·57 per cent. of all radial loops being found upon second fingers only (Table II).

Although the statistical difference of pattern-types between right and left hands is found to be less evident on the second finger than on digits I, IV and V, it is interesting to note that also here a difference exists, the functionally most effective patterns (radial loops and arches) showing a considerable surplus on right hands. What has been said here about digit II is valid, to a certain degree, also with regard to the third finger. Also here we find the finger applying its radial side when, together with digit II, opposed to digit I, and also here we find the percentage of arches considerably above the average (11·03 per cent. to the average 7·4 per cent., Table I). The radial loops, however, so peculiar to the second finger, are here much less frequent (2·31 per cent. of the fingers), even if still more so than on digits IV and V.

The two questions raised at the beginning of this chapter with regard to the statistical peculiarities of digits I and IV as well as to those of digit II may, according to the above discussion, as a working hypothesis, be explained partly as results of a historical development of apical pads and of their papillary patterns and partly also as an adaptation to their function in the human race, the first view being above all valid for the frequency of whorls upon digit I and especially upon digit IV, the second for the predominant occurrence of arches and radial loops upon digit II.

The explanation here suggested refers to the statistical peculiarities occurring similarly in all the human races as yet investigated. But we have found also on certain points characteristic differences between the statistics of the various races. Such was the case with the absolute frequency of whorls, being upon each of the fingers very considerably greater in the races of Eastern Asia than in those of Northern Europe; and such was the case also with the occurrence of arches and radial loops being, especially on digit II, very much more frequent in the hands of the last-named races. Also these differences ought, if our working hypothesis shall prove efficient, to find their explanation from the two points of view above-mentioned. A racial difference may exist with regard to the constancy of elevation of the apical pads, and therefore also with regard to the frequency of whorls upon the various digits, and a racial difference may exist also with regard to the functional adaptation

of digit II, some races using more the front of this finger-ball, while in others its radial side plays a greater part.

Féré (1896) has, through experiment, demonstrated that the position of the various fingers, e.g. in grasping a ball, differs from one person to another as well as from right hand to the left, but at the same time that one and the same hand always grasps the ball in the same way. It must, however, be left for future investigations to decide whether races differ in this respect.

Till now we have treated the statistics of the human *hand* only. Before finishing this discussion it will, however, be of interest to glance also at the statistics of Hasebe (1918) as to the apical patterns of the *feet* of 100 individuals from Japan.

Dig.		I		II		III		IV		V		All
Feet		r	l	r	l	r	l	r	l	r	l	Both
Whorls		4	10	18	13	53	50	11	12	0	1	17,2 %
Loops	Tib.	3	6	0	5	0	0	0	2	0	2	1,8 %
	Fib.	77	67	76	68	42	39	73	63	46	41	59,2 %
	Total	80	73	76	73	42	39	73	65	46	43	61,0 %
Arches		16	17	6	14	5	11	16	23	54	56	21,8 %

TABLE X. Apical patterns of the feet, in percentage of toes, of 100 Japanese. (Hasebe, 1918.)

The *statistics of the feet* give, as will be seen from Table X, results surprisingly different from those of the hands of the same race, the percentage of whorls (17·2 per cent.) being very much lower, that of the loops (61 per cent.) being higher than the corresponding figures of the hands. The most surprising feature is, however, the very frequent occurrence of arches (21·8 per cent.) among the apical patterns of the feet, while this pattern-type upon the hands is relatively very rare.

The distribution of each pattern upon the various toes proves also to be very characteristically different from that of the fingers. The whorls show a great maximum upon third toes of both right and left feet (*ca.* 50 per cent.), sinking rapidly towards both sides, very differently from their distribution on the hands with the typical maxima upon digits I and IV. The arches are in their distribution no less particular,

finding their minimum of occurrence on second and third toes, while the corresponding fingers carry the greatest number of the same pattern. On the fifth toe the arches reach their highest frequency, being found upon this toe in 55 per cent. of all feet. Radial loops on the feet are exceedingly rare, while the ulnar loop is here by far the most common pattern, showing minima upon the third toe, caused by the great frequency of whorls, and on the fifth, the loops here giving place to the arches.

Looking upon the apical patterns of the feet from the same points of

Fig. 8. Right palm of *Lemur brunneus*. (Schlaginhaufen, 1905 *a*, Fig. 64.)

view which we used in the case of the hands, we find here a very far-reaching reduction of the typical pattern, the whorl, giving as a result the high percentage of arches. The third toe only has for some reason kept the original pattern with a great constancy. Many questions might be raised, phylogenetic as well as functional, from a consideration of these statistics of the feet, but our material is as yet too scanty for really discussing any of these questions.

For a full discussion of the statistics of pattern-types it would be of great interest to consider also the results reached by various authors with regard to the apical patterns of Prosimians and Apes. Such extension of the discussion would, however, be of little value from the

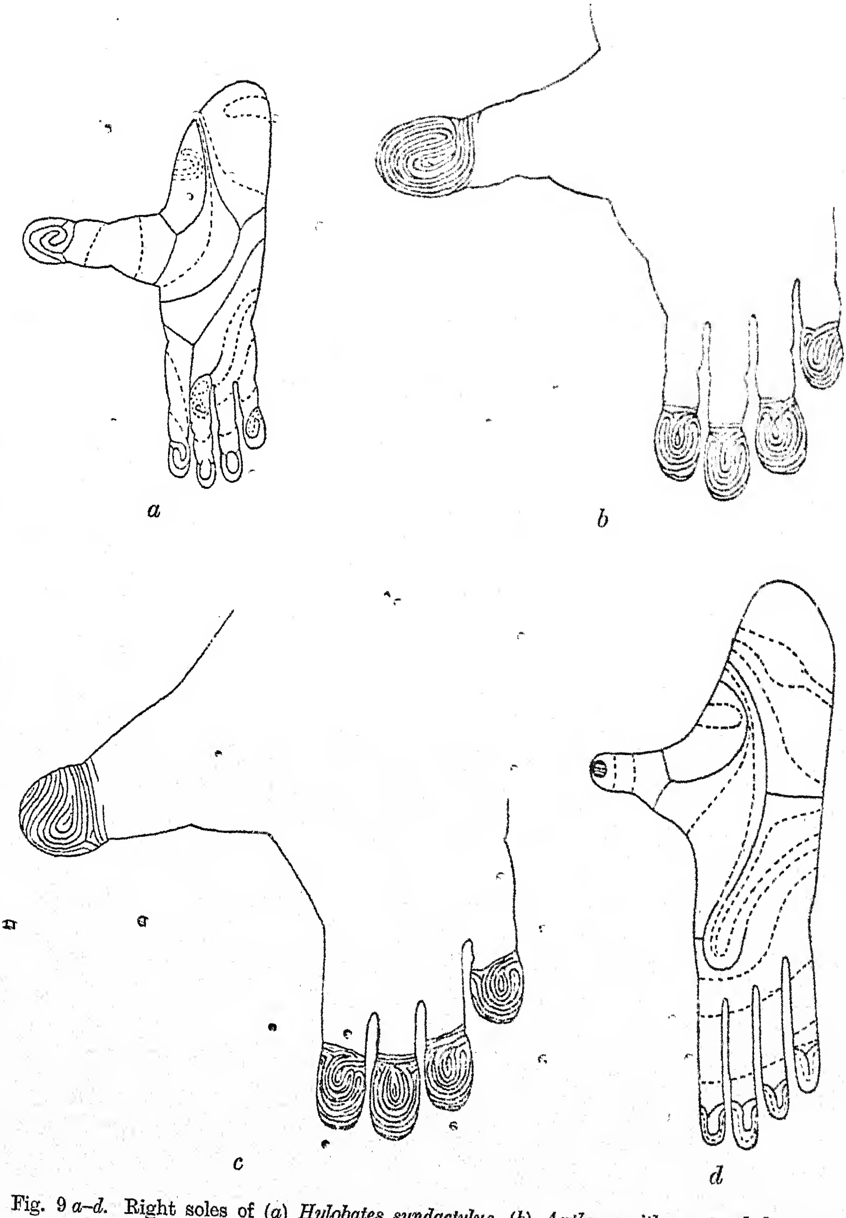


Fig. 9 *a–d.* Right soles of (*a*) *Hylobates syndactylus,* (*b*) *Anthropopithecus troglodytes,* (*c*) *Gorilla gorilla,* (*d*) *Simia satyrus.* (Schlaginhaufen, 1905 *a*, Figs. 147, 166, 171 and 174.) Fig. 9 *d* is drawn by Schlaginhaufen according to the description previously given by Alix.

standpoint of heredity, and therefore lies outside the scope of this paper.

Referring especially to the comparative review of this matter by Schlaginhaufen (1905) and to Figs. 8–9 of this paper, I shall here mention a few points only which may be of interest also for our consideration of human patterns. Such points are:

(1) The gradual development from the longitudinal striae of apical patterns of Prosimians (Fig. 8) into the more complicated patterns of *Hylobates* and other apes, especially those of the Anthropoids. Among the latter, however, a reduction, similar to that found also on human fingers, is seen to have taken place above all in the apical patterns of the Orang-Utan (Fig. 9 *d*).

(2) The relatively very high percentage of whorls, this pattern-type giving in *Hylobates* as well as in the higher apes a very considerable surplus over that of the loops, and a very low percentage of arches, which in most species investigated do not occur at all.

An exception is, as already mentioned, formed by the Orang-Utan, on the apical patterns of which whorls are very rare, while loops and a so-called "triangular type" (Alix, 1868), very similar to the "tented arch" of modern classification, represent the predominating patterns (Fig. 9 *d*).

(3) A narrow elliptical shape of the whorls ("Simian type" of Kollmann), and a more or less distinctly longitudinal course of the ridges also of other pattern-types ("Fig. tensae," Schlaginhaufen). This same longitudinal course is shown also in the just-mentioned "tented" arches of the Orang-Utan.

CHAPTER 4.

ANALYSIS OF FINGER-PATTERNS.

Through the statistics of the preceding chapters we have reached a general view of the characteristic distribution of papillary patterns, and through this also of the characteristics of each special finger with regard to the statistical occurrence upon it of the various pattern-types. With this knowledge we may now discuss the question of inheritance of finger-patterns.

The material for my investigations upon this point consists of the finger-prints, taken for this special purpose, of some 200 Norwegians. These represent partly single persons, but mostly whole families containing two or three generations. They are an arbitrary collection of

family material, no selection having been made with regard to civil position, age, etc. of the individuals[1].

Before entering into a discussion about heredity it will be necessary to find some basis for a comparison of different papillary patterns with

a
Nr. 1, 7; Dig. II *l.*

b
Nr. 1, 7; Dig. II *r.*

c
Nr. 1, 7; Dig. IV *r.*

d
Nr. 1, 7; Dig. III *r.*

e
Nr. 1, 7; Dig. V *r.*

Fig. 10 *a–e*. Photographs of finger-patterns showing transitions from one pattern-type into another. Explanations in the text. Most of the patterns here demonstrated are taken from individuals also represented in the pedigrees of Fig. 23 and Pls. III and IV, the family-number of each individual being found below the pictures together with an indication of the finger on which the pattern is found. *r*, right; *l*, left hands.

each other, more fit for our purpose than that of the practical classification.

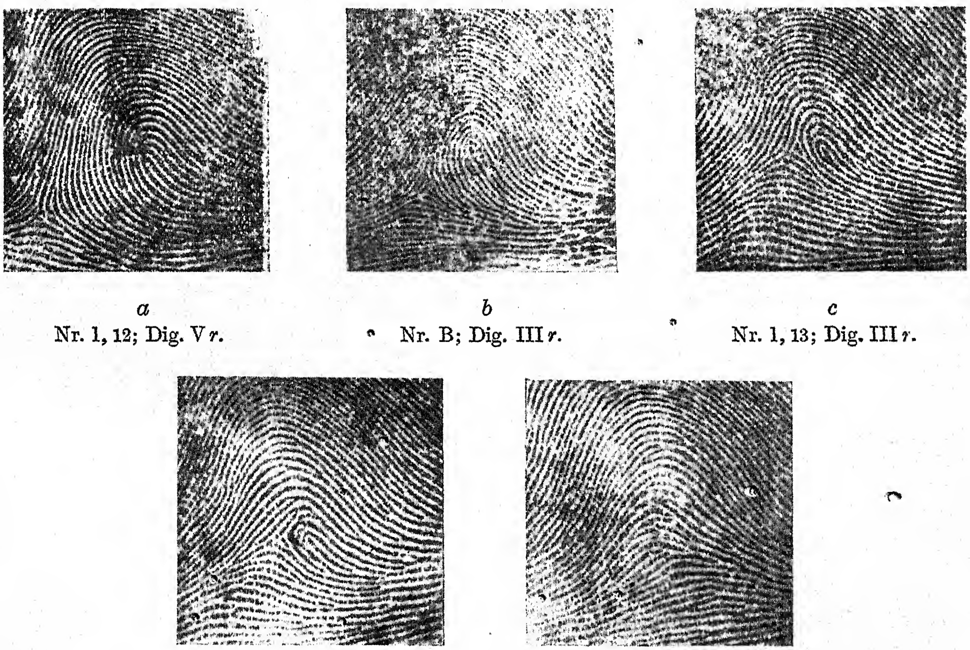
As already shown by Whipple (1904) transitions are found between

[1] My collection of finger-prints has been constantly augmented during my investigation. For this reason the number of individuals used for tables and curves is, as will be seen, not always the same.

whorls and loops as well as between loops and arches. Such transitional patterns are indeed very numerous, and a thorough analysis proves, very often, the likeness between, e.g., a loop and a whorl to be much more close than that between two different whorls. The classification of Galton, which has proved so useful in practical application, does not, therefore, give a sufficiently clear and detailed expression of the natural relationship between different patterns.

In order to find a new basis of classification, suitable for our purpose, it may be well first to study some series of patterns met with in nature, and illustrating the gradual transition from one "type" into another.

In Fig. 10 *a–e* a series of patterns is shown—all found on the digits of one and the same person[1]—which illustrates the transition from a typical whorl into a loop. In the first picture (10 *a*) the whorl is seen to



a Nr. 1, 12; Dig. V *r*.

b Nr. B; Dig. III *r*.

c Nr. 1, 13; Dig. III *r*.

d Nr. 1, 12; Dig. III *r*.

e Nr. 1, 12; Dig. III *l*.

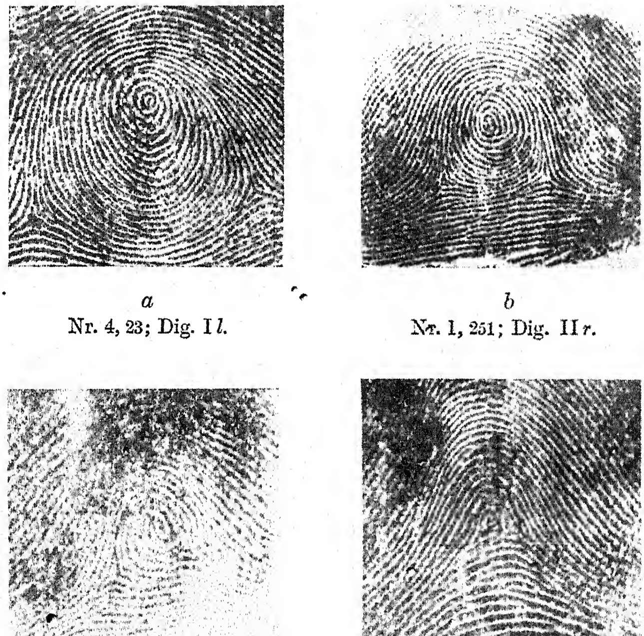
Fig. 11 *a–e*.

be nearly symmetrical, although its two triradii are not precisely at the same distance from the centre of the whorl; on the left side of the

[1] The figures below the patterns of Figs. 10–17 refer to individuals marked with the same figures on the pedigrees of Fam. 1–6.

figure the two points are separated by 18 ridges, while on the right side only by 13. In the preceding photographs (Fig. 10 *b–d*) we see the right side of the whorl being reduced, the distance between the triradius and the centre gradually diminishing until in Fig. 10 *e* we find a mere loop.

A further reduction of the pattern is seen in Fig. 11 *a–e*, showing transitions between a loop and an arch characterised by a gradual diminution of the distance between the core of the loop (the top of its axis) and the only triradius existing in this pattern.



a Nr. 4, 23; Dig. I *l*.

b Nr. 1, 251; Dig. II *r*.

c Nr. A; Dig. II *r*.

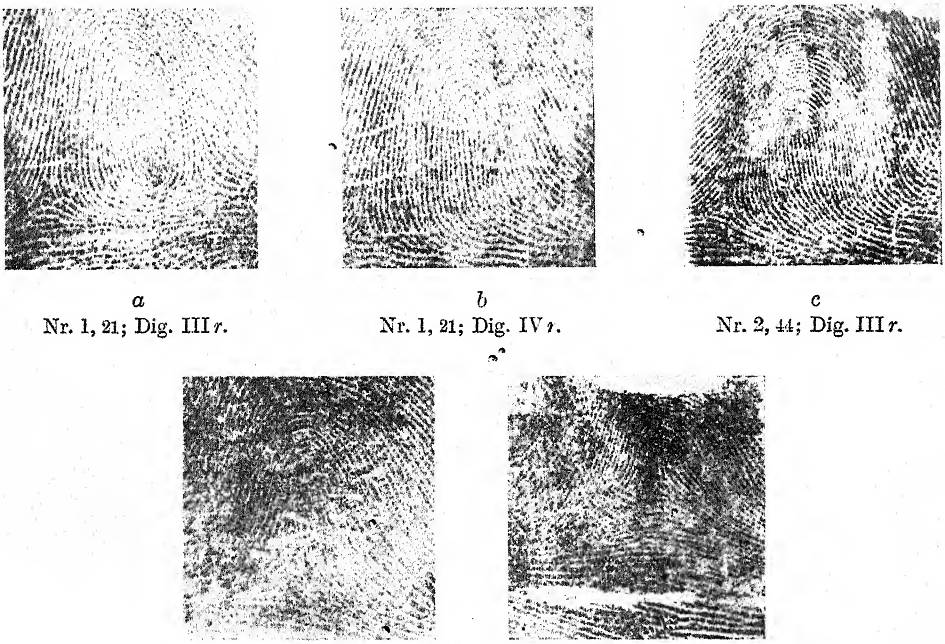
d Nr. 2, 23[1]; Dig. IV *r*.

Fig. 12 *a–d*.

The transitions between whorls and arches do not, however, necessarily lead through the loop-stage. Pictures are also found in which the whorl is reduced contemporaneously on both sides, the distance between centre and triradii being more or less diminished, while the symmetry of the whorl in such cases may be kept during the whole process (see Fig. 12 *a–d*).

Fig. 13 *a–e* illustrates once again some forms of transition between

whorl and arch, corresponding to those of Figs. 10–11, but characterised by the long elliptical shape of the whorl ("Simian type" of Kollmann and Schlaginhaufen) which is, as will be shown below, peculiar to and inheritable within certain families. The longitudinal character is seen to be kept not only in the whorl (Fig. 13 *a*) but also in the loops (*b–c*) and even in figures forming a transition between loop and arch (*d–e*). The latter figure represents the so-called "tented arch" of the practical



a Nr. 1, 21; Dig. III *r*.
b Nr. 1, 21; Dig. IV *r*.
c Nr. 2, 44; Dig. III *r*.
d Nr. 1, 25; Dig. II *l*.
e Nr. 1, 252; Dig. II *l*.

Fig. 13 *a–e*.

classification and it is not unlike the pattern found on the end phalanges of an Orang-Utan (Fig. 9 *d* of this paper).

Besides the more or less circular whorl and the ellipsis just considered, we often find the whorl formed as a double spiral (Fig. 14 *a*), which, through a loosening of its windings, may be transformed into a double loop (Fig. 14 *b–c*), that is, two separate loops, the axes of which are more or less spirally twisted round each other. ("Twinned loops" and "lateral pocket loops" of the practical classification.)

Also in whorls of this kind any number of transition pictures may be

a
Nr. 1, 12; Dig. IV *r*.

b
Nr. 1, 13; Dig. I *l*.

f
Nr. 1, 13; Dig. I *r*.

c
Nr. 1, 12; Dig. I *l*.

g
Nr. 1, 12; Dig. II *r*.

d
Nr. 1, 13; Dig. II *l*.

h
Nr. 1, 12; Dig. I *r*.

e
Nr. 1, 12; Dig. II *l*.

i
Nr. 1, 13; Dig. II *r*.

k
Nr. 1, 12; Dig. III *l*.

demonstrated, the transition here following several different lines. Some of these lines are shown in Figs. 14–16.

As seen from Fig. 14 *b–d* and *f–h* one of the two loops may seem reduced while the other still exists in full size, a transition, thus, between the original whorl and a loop; the latter will, however, in such cases have a shape characteristically different from ordinary loops, its axis still being more or less curved in the direction of the original spiral twisting (*d* and *h*). From such loops further transition stages will be found (Fig. 14 *e* and *i*) leading to a typical arch (Fig. 14 *k*).

In Fig. 15 a case is demonstrated in which both loops appear reduced simultaneously.

Fig. 15.

Fig. 16, further, shows the transformation of a double loop (*a*) in two diverging lines. The first line (*b–c*) is not essentially different from the pictures of Fig. 14, both loops appearing more or less checked in their development until the arch is reached; but in the other line (*d–e*) we find a transition into a typical loop in a way conspicuously different from that of Fig. 14. In this case the two loops of the original pattern (*a*) are in their reduced state more or less intimately joined to form a single loop (*e*). This process is, as seen from Fig. 16 *d*, characterised by a transition stage in which the upper loop forms, as it were, a mantle round the top of the lower one. "Mantle" and "inner loop" are in such figures easily distinguishable from each other, their ridges having on the concave side of the loop a conspicuously different direction.

Pictures like that of Fig. 16 *d* have been described already by Schlaginhaufen (1905) as common in *Hylobates* and other Primates. His description reads as follows (p. 73): "Die betreffende Figuren bestehen somit aus drei ineinander geschachtelten Systemen: (1) Fasciculi proprii, die einen Sinus mit nach dem Fibularrand umbiegenden Crura oder mit fibulo-proximal gerichteten Achse darstellen, ferner Fasciculi peri-

pherici, welche sich in ein inneres System von Sinusbogen mit konvergenten Schenkeln und (2) ein äusseres von Sinuslinien, die den Fasciculi proprii parallel verlaufen, gliedern. Diese Fig. tact. erreicht ja nach dem

a
Nr. 1, 43; Dig. I *l*.

b
Nr. 1, 43; Dig. I *l*.

c
Nr. 1, 43; Dig. I *l*.

d
Nr. 1, 43; Dig. III *l*.

e
Nr. 1, 43; Dig. V *l*.

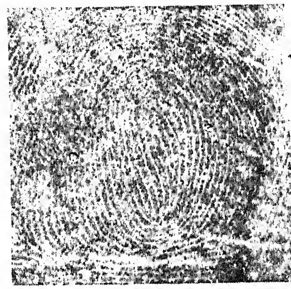
Fig. 16 *a–e*.

Grad ihrer Ausbildung grössere oder kleinere Ähnlichkeit mit dem Vortex duplicatus."

This description by Schlaginhaufen of the Fig. tactiles of *Hylobates* may be literally applied to our pictures.

The double loops above demonstrated all belong to a broad circular type of patterns corresponding to those which, according to Whipple

a
Nr. 1, 25; Dig. I *l.*



b
Nr. 1, 2^1; Dig. IV *r.*

c
Nr. 1, 2^1; Dig. IV *l.*

d
Nr. 1, 23; Dig. IV *l.*

e
Nr. 1, 253; Dig. IV *l.*

f
Nr. 1, 251; Dig. III *l.*

Fig. 17 *a–f.*

(see Fig. 5 of this paper), should have arisen through a flattening of the pad. But in the ellipsoid whorls also a tight twisting of two independent

loops may at times be seen, the twisting here, however, not essentially changing the longitudinal direction of ridges in the central part of the pattern (Fig. 17 *a*).

Fig. 17 *b–f* shows, finally, a series of transition figures between such an ellipsoid double loop and the typical single loop, the transition here being realised through a narrowing of one of the loops at the base of its last turn, the top of the latter thus being included as a more or less reduced nucleus between the central turns of the other.

Double loops of this ellipsoid kind correspond very closely to the apical pattern of a Chimpanzee figured by Kollmann (1883, Fig. 37), who

Fig. 18. Apical pattern (digit III *r.*) from a Chimpanzee. (Kollmann, 1883, T. II. Fig. 37.)

mentions that the same longitudinal pattern may also be found upon human fingers. This pattern, representing the "Simiadentypus" of Kollmann, is reproduced in Fig. 18.

An attentive consideration of the figures shown in Figs. 10–17 proves

(1) That the shape of the whorls, as well as of the loop, of human fingers may be either more or less circular (Figs. 10–12) consisting of curved ridges only, or it may form a more or less narrow ellipsis (Fig. 13) with approximately straight, longitudinal lines in its central part ("Simiadentypus" Kollmann; "Fig. tensae" of Schlaginhaufen).

(2) That, in both types mentioned, the whorl may appear to consist of a double loop (Figs. 14–17) the two members of which are more or less tightly twisted round each other. The tendency to twisting may be more

or less conspicuously expressed on the various fingers, more on digit I than on any of the others.

(3) That from any whorl—circular or elliptic, twisted or untwisted—series of transition pictures may be found leading along different lines down to the most reduced pattern-type, the arch. Within each of these series the stage of transition represented by a pattern may be characterised as its *quantitative value.*

(4) Of importance for our discussion of heredity is, finally, the fact that *such transition series are found, not by combining patterns from arbitrarily selected persons but by considering different fingers of one and the same person, or of persons nearly related to each other, or at least belonging to families carrying the same type of patterns.* Thus, Fig. 10 *a–e* all belong to one person (Nr. 1, 7), Fig. 13 *a–e* are taken from two families (Fam. 1, 2 and Fam. 2) with very similar elliptic patterns, Fig. 14 *a–k* give patterns from the fingers of a pair of identical twins (Nr. 1, 12 and 1, 13). Such is the case also with Fig. 11 with exception of the pattern *b* taken from a person not forming part of our family schemes. It is of interest here to see that even if this pattern, the loop of Fig. 11 *b*, forms with regard to size and development a good transition picture between *a* and *c*, it can, after all, be easily distinguished from the others through the breadth of and the distance between the ridges, through the steepness of the peripheral part of the loop, etc. The full harmony of this series is broken through this introduction of a strange pattern into the series taken from the fingers of the pair of identical twins.

Further, Fig. 16 *a–e* are taken from a father and two of his sons, and Fig. 17 *a–f*, finally, belong to persons representing three generations of one and the same family. The series of Fig. 12 *a–d* only, the patterns of which are rather rare, is combined from the finger-prints of different families.

An attentive consideration of such harmonious series of transition formed by patterns belonging to nearly related individuals cannot but give the impression, that *each series represents in the main one and the same genotypical design, which proves, however, in the various patterns to be more or less checked in its realisation*; that is, the *quantitative value* of a pattern, its degree of development, may vary independently of its design. A clear demonstration of this fact is seen especially in Fig. 14 *a–k*, the design of each pattern here being so closely the same, that the central part of any pattern might without difficulty be made to fit into the peripheral part of any of the others, which would be quite impossible if a central part from a pattern of Fig. 14 were placed in connection with the

patterns of e.g. Figs. 13 or 17, or even with those of Fig. 16, which show upon the whole a design very similar to that constituting the patterns of Fig. 14 (cf. Figs. 14 *b* and 16 *a*).

That such independence between the design of the patterns and their quantitative value is reversible, is easily seen in a comparison of e.g. Figs. 16 *a* with 17 *a*. Both patterns exhibit well-developed double loops, that is, similar quantitative values, but their designs are very different, one being of an elliptical, the other of a broad circular shape.

Further analytical results will be reached by comparing, e.g., Figs. 12 *a* and 16 *a* or Figs. 13 *a* and 17 *a*. Both these pairs of patterns present well-developed whorls, that is, the quantitative value is similar in all of them. The two members of each pair show also either the circular (Figs. 12, 16) or the elliptical (Figs. 13, 17) shape of pattern. But, after all, the two members of each pair are very conspicuously different, one of them showing in each case a regular whorl, while in the other a tendency of twisting has impressed the whole character of the pattern.

The result of our analysis of finger-patterns is, therefore, that *in their phenotypical appearance at least three different characters are found, varying independently of each other*, viz. (1) the quantitative value of the pattern, meaning the degree of development of its design, the latter being again determined through (2) the shape (circular-elliptical), and (3) the twisting tendency of the ridges.

The hereditary nature of one of these characters, the circular or elliptical shape of apical patterns, is strongly indicated through the occurrence of the elliptical shape within certain families only. The question about the heredity of the two other characters is not so easily answered. It has, however, been thoroughly investigated and will be discussed in the following chapters[1].

CHAPTER 5.

Methods of Classification.

According to the results of our analysis of finger-patterns it has proved necessary for a full comparison between them to work out a method of classification which will give an adequate expression of their quantitative value, and which will give a sufficiently clear definition also of the shape of patterns, whether it should be called circular, elliptic, or perhaps be characterised as median between both these extremes.

The *twisting-tendency*, which, if present, can be directly observed,

[1] Short preliminary accounts of this investigation have been given by me in 1923 (*b*, *c*).

and the radial or ulnar direction of the pattern should, for a comparison between them, also always be noted.

As a basis of classification has been used the method of ridge-counting, previously applied to loops only. This method has here been developed for application to other patterns in the way now to be described.

The *quantitative value* of any pattern is expressed in two figures based upon the number of ridges between each of the two triradii and the centre of the pattern (the centre of a typical whorl, the core of a loop, the two cores of a double loop). If there exists only one triradius (loops) the figure of the other side is 0; if no triradius exists (simple arch) the figures of the pattern are 0–0.

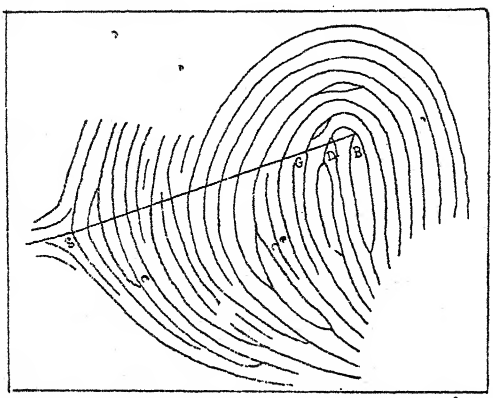


Fig. 19. Ridge-counting; 17 ridges counted. (Henry, 1901, Fig. 37.)

The figure representing the radial side of the finger (the left side of a print from a right-hand finger, the right side of a left-hand one) is always written first.

As general rules of ridge-counting may be cited from Henry (1901), p. 45:

"In *ridge-counting* it must be remembered that the *two terminal points are excluded from count,* that ridges like *G* (see Fig. 19 of this paper), which run close up to without meeting the line *SB*, are also excluded, and that when two ridges result from a bifurcation as at *D*, close to the line *SB*, both are counted."

Irregularities of the pattern such as those just mentioned will, of course, influence the result of the counting without essentially influencing the real distance between triradius and core.

In order to diminish the effects of such irregularities the results reached by counting the ridges are not directly used for expressing the distance

between triradius and centre; but they are grouped to classes marked 0–10 and distinguished as follows:

	No. of ridges	Class
Triradii none	—	0
„ 1–2	0	1
„ „	1–2	2
„ „	3–4	3
„ „	5–6	4
„ „	7–8	5
„ „	9–10	6
„ „	11–13	7
„ „	14–16	8
„ „	17–20	9
„ „	>20	10

Both sides of a pattern being classified in this way the quantitative value of the finger is found by adding the two class-values and dividing their sum by 2. A large ulnar loop, with, for example, 18 ridges between triradius and core (see Fig. 20), will thus, on its radial side belong to class 9 while on the ulnar side where no triradius exists, it belongs to class 0. The quantitative value of this loop, therefore, will be

$$\frac{9+0}{2} = 4{\cdot}5.$$

Fig. 20. Determination of quantitative value of a loop. Number of ridges, 18–0; Classes, 9–0; Value, 4·5.

In Pls. I–II a series of examples are given which will illustrate the classification of patterns.

A pattern is considered radial when its ridges, or at least part of them, run out parallel towards the radial side of the finger, or in other words when the only triradius (in loops) or the one which has the greatest distance from the centre (in whorls) lies at its ulnar side. Thus expressed the rule may be applied also to double loops.

In ulnar patterns the triradius in question is found upon the radial side.

The quantitative value of a pattern being determined, its figures also give an expression of the direction: if the first, radial, figure is the lower one, the pattern is radial, and *vice versa*.

The *shape* of a pattern is in extreme cases very easily distinguished. The long elliptic shape with straight longitudinal lines in the central part of the pattern, the so-called "Simian type," is without difficulty recognised in whorls as well as in loops (Fig. 13), and also in double loops (Fig. 17) as essentially different from the more common, broad circular patterns (Figs. 10–12, 14–16).

A line of distinction should be drawn, however, between the two groups, clear enough to separate them also in more doubtful cases.

The same characteristic pattern-shape of an individual being usually realised in loops as well as in whorls, the distinction should further be applicable to patterns of both types.

After many attempts at finding the right method I have selected

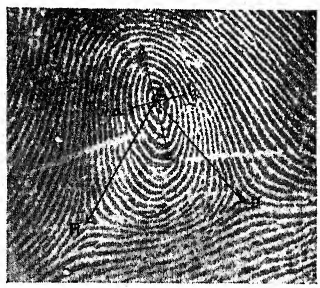


Fig. 21. Determination of quantitative value and shape of a whorl. *R*, radial side; *C*, centre. Qu. val.: ridges 15–15; class 8–8; value 8. Shape: (5 ridges counted from the centre (*C*) along each arm of the cross) breadth $(a–b) = 11{\cdot}5$ mm.; height $(c–d) = 18$ mm.; shape-index: $\frac{B}{H} < \frac{2}{3}$; elliptic (*E*).

the one described below, as giving a fully satisfactory distinction between typical elliptic patterns on one side and the median and circular patterns on the other. Between the two latter shapes distinction can be made in the same way.

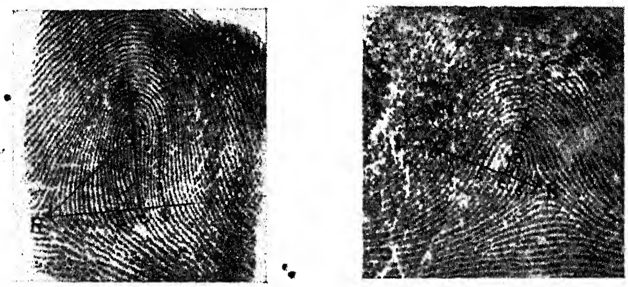
The methods used for determining the shape of patterns consist in finding an adequate expression of the relation between breadth and height of the pattern. This has been done in whorls by drawing a cross through the centre of the pattern, one arm of this cross following the longitudinal, the other the transverse axis of the whorl, and further by counting a certain number[1] of ridges (e.g. 5) from the centre along each of the four arms (see Fig. 21). The distances between the points thus reached (*a–b*,

[1] The number counted may vary somewhat (4–8) according to the size of the patterns.

c–d) are measured in millimetres, and the proportion between breadth and height $\left(\frac{B}{H}\right)$ of the cross is noted as the shape-index.

For loops the following method has been used:

A line is drawn from the triradius across the ridges of the loop and at right angles to their direction (Fig. 22). Upon this transverse line the intersection with the axis of the loop (*c*) is marked, and a certain number of ridges are counted from this point along the line in both directions. The distance between the two points thus marked (*a–b*) is taken as an expression of the breadth of the loop.



a *b*

Fig. 22 *a–b*. Determination of quantitative value and shape of loops. Signification of letters as in Fig. 21. *a*. Qu. val.: ridges 19–0; class 9–0; value 4·5. Shape: breadth (*a–b*) = 10 mm.; height (*c–d*) = 23 mm.; shape-index $\frac{B}{H} < \frac{3}{5}$; elliptic (*E*). *b*. Qu. val.: ridges 6–0; class 4–0; value 2. Shape: breadth (*a–b*) = 9 mm.; height (*c–d*) = 9 mm.; shape-index $\frac{B}{H} > \frac{3}{4}$; circular.

Then, starting from the point farthest from the triradius (*b*) a ridge is traced towards the top of the loop until its intersection (*d*) with a perpendicular erected upon the transverse line (*a–b*) in its middle point (*c*). The distance between *c* and *d* represents the height (*H*) of the loop in question, and the proportion between *B* and *H* gives, as in the whorls, an expression of its shape-index.

Experience has shown that the proportion of a loop, found in the way just described, gives an expression of its shape very closely corresponding to those of the whorls, so that if the proportion between *B* and *H* is the same in a whorl and in a loop we may be confident that the two patterns can be characterised as representing also the same shape.

For typical whorls and loops, therefore, one and the same scale may be used in determining their shape:

If $\frac{B}{H} > \frac{3}{4}$ the pattern is called *circular* (C).

If $\frac{B}{H} = \frac{3}{4} - \frac{2}{3}$ „ „ *median* (M).

If $\frac{B}{H} < \frac{2}{3}$ „ „ *elliptic* (E).

Examples of shape-determination are found on Pls. I–II.

For irregular and atypical patterns as well as for double loops, the method here described cannot be used; but practically always two or three fingers of each hand, especially those of digits III–V, will be found with patterns typical enough to determine the characteristic pattern-shape of the person in question. Very often we find also, that patterns which cannot be exactly measured may, according to their whole outlines, whether broad or narrow, after all be characterised as being of either the circular or the elliptical shape.

Such is the case also with highly reduced patterns, as arches and very small loops, their elliptical design making itself apparent in a high and narrow shape of the loop, and a so-called "tented" shape of the arch.

A twisting tendency, most fully developed in the double loops, may, as already demonstrated (Figs. 14–17), be found in circular patterns as well as in the elliptical. Such a tendency will, even when less developed, be recognised by direct observation of the pattern in question. Its presence is revealed through a T, which, together with the shape-characteristics (C or E) will give the full expression of the design of the pattern.

The results of an analysis of finger-prints from a series of persons will after application of the above methods for determining the quantitative value, the direction and the design of each pattern, give a picture like that of Table XI, every vertical column of the table containing for each of the ten fingers of a person the three characteristics just mentioned.

Through a comparison of the results found for the various fingers, the characteristics of the individual are then determined.

The following rules ought here to be remembered:

(1) The quantitative value of an individual is found by adding the values of the ten fingers. The finger-values varying between 0 and 10, the quantitative values of individuals will, consequently, have a range of variation between 0 (individuals with simple arches on all fingers) and 100 (fully developed whorls on all fingers).

(2) The shape, circular or elliptical, is determined through a comparison of the shape-indices of the fingers, special attention here being

paid to digit IV, partly also digits III and V, as the most representative fingers with regard to pattern-shape. The reason for such preference of digit IV is seen in the fact that upon this finger the pattern-design is usually most fully developed (cf. the large number of whorls upon digit IV, Tables I–II, VI). The broad and flattened ball of digit I very often causes some deviation also in the design of its pattern, while upon digit II the great number of arches, that is, of very low-valued patterns, characteristic to this finger (cf. Tables I–II, VII) very often makes it unsuitable for serving as a basis of shape-determination.

(3) Tendency to twisting is notified as a characteristic of the individual *when visible in any one of its finger-patterns.*

(4) With regard to the direction of finger-patterns, radial or ulnar, my results, both statistical and analytical, have proved this to be a characteristic of fingers (radial patterns on digit II, Tables I–II, IX A) much more than of individuals. The question will be discussed in a following chapter (Chap. 6 *c*) showing some indications of heredity with regard to pattern-direction. But, so far, I have not found reason to consider it as one of the typical individual characteristics.

Remarks on Table XI.

As described in the text (p. 49) the quantitative value of a pattern is given by two figures representing the class of the radial as well as of the ulnar side of the pattern, the figure 0 meaning that no triradius exists upon the side in question, while the highest figure 10 means that more than 20 ridges lie between a triradius and the centre of a pattern. 10–10, therefore, is the value of a fully developed symmetrical whorl, while 0–0 is that of an arch without any triradius. Arches may exist in which one, or even two triradii occur, but in this case no ridge must intervene between triradius and centre. The highest value of an arch, therefore, will be 1–1. All patterns in which one side has a value of from 2 to 10, while its other side is marked 0, are loops, these patterns having only one typical triradius on the side opposite to the opening of the loop.

The quantitative value of an individual is found by summing up the class-figures of all the fingers and dividing this sum by 2. The lowest value of a person will, therefore, be 0—a value implying the figures 0–0 for each of the ten fingers. If, on the contrary, all fingers are marked 10–10, the highest value of an individual, viz. 100, is reached.

The direction of a pattern, that is, its opening towards the ulnar or radial side of the finger, is noted by *U* or *R* for all patterns which are not strictly symmetrical (*S*). This character is expressed already by the figures of the quantitative value, the figure of the radial side being always written first and the pattern opening towards the side which has the lowest value.

The shape of a typical pattern is determined by the proportion between its breadth and height, the shape-index, $\frac{B}{H}$, being noted for each finger, if determinable. The shape is called circular, *C*, if $\frac{B}{H} > \frac{3}{4}$. If it is $< \frac{2}{3}$ the pattern is called elliptic, *E*; between these border-lines we find a median shape, called *M*. Any of these pattern-shapes may be com-

plicated through a twisting tendency, the ridges forming double spirals, "twinned loops," "lateral pocket loops" or, in low-valued patterns, indications of such design. Any trace of a twisting of ridges is expressed by *T*.

Finger	Hand	Characteristics	Nr. 19, E. G. b. 1895 ♀	Nr. 21, T. B. b. 1907 ♂	Nr. 24, J. S. b. 1892 ♂	Nr. 10, M. B. b. 1886 ♀	Nr. 17, A. B. b. 1862 ♂	Nr. 3, G. R. b. 1882 ♀	Nr. 7, C. S. b. 1862 ♂
I	r	Qu. Val., Direct.	9-0 U	8-8 S	9-8 U	7-0 U	10-10 S	2-0 U	10-10 S
		Shape B/H	C. 5/2	Tc	E 7/11	C 7/4	C 10/10	C	C 8/9
	l	Qu. Val., Direct.	7-0 U	7-8 R	7-10 R	3-2 U	10-4 U	0-0 S	10-10 S
		Shape B/H	C 6/3	Tc	E 6/10	T	Tc	C	C 8/9
II	r	Qu. Val., Direct.	7-0 U	6-9 R	9-0 U	5-0 U	5-10 R	0-0 S	9-10 R
		Shape B/H	C 6/5	C 5/5	E 5/8	C 7/3	C 6/7	C	M 8/11
	l	Qu. Val., Direct.	6-0 U	7-8 R	5-5	0-0 S	8-10 R	0-0 S	8-10 R
		Shape B/H	C 5/3	Ct 5/6	E, 5/10	C	C 6/7	C	M 7/10
III	r	Qu. Val., Direct.	6-0 U	10-9 U	9-7 U	4-0 U	10-10	0-0 S	8-0 U
		Shape B/H	C 5/4	C 6/7	E 5/10	C 6/4	C 8/10	C	E 5/8
	l	Qu. Val., Direct.	6-0 U	9-6 U	7-8(?) R	5-0 U	10-10 S	5-0 U	8-7 R
		Shape B/H	C 4/3	Tc	(Scar)	C 5/3	C 6/7	C	Et 6/12
IV	r	Qu. Val., Direct.	8-0 U	10-9 U	9-0 U	4-0 U	10-10	2-0 U	9-0 U
		Shape B/H	C 5/3	C 6/7	E 5/9	C 6/4	C. 7/9	C	E 5/10
	l	Qu. Val., Direct.	7-0 U	10-7 U	9-0 U	0-0 S	10-10 S	3-0 U	9-4 U
		Shape B/H	C 3/3	C 5/6	E 6/11	C	C 7/8	C	Et
V	r	Qu. Val., Direct.	7-0 U	9-5 U	9-0 U	4-0 U	9-8 U	2-0 U	8-0 U
		Shape B/H	C. 5/3	C 5/6	M 5/7	C	C 6/7	C	E 5/8
	l	Qu. Val., Direct.	7-0 U	9-0 U	7-0 U	2-0 U	10-8 U	3-0 U	9-0 U
		Shape B/H	C 4/4	C 4/4	M	C	C 7/8	C	E 5/9
		Characteristics of Individual	70/2 = 35 C	154/2 = 77 C.T.	118/2 = 59 E	36/2 = 18 C.T.	182/2 = 91 C.T	17/2 = 8,5 C	139/2 = 69,5 E.T.

TABLE XI. Determination of pattern characteristics of individuals (with explanation).

Each vertical line of the table represents the ten fingers of a person investigated, the characteristics of the individual being found below.

L. Nr. 19, E. G. (first vertical line). The analysis of the finger-patterns here gives no difficulty. All patterns are typical ulnar loops, large enough to be measured for exact determination of their shape and quantitative value. The person is marked *C*, 35.

L. Nr. 21, T. B. The figures of the quantitative value prove the existence of well, though not quite fully, developed whorls upon all fingers but one, the left digit V carrying a large ulnar loop. One of the whorls (8–8) is symmetrical, three others are radial, while the six remaining patterns are all ulnar. All patterns are circular, but no less than three of them (*Tc*) form double loops, the twisting tendency appearing also in one of the more typical whorls (*Ct*). This individual is marked *CT*, 77.

L. Nr. 24, J. S. gives an example of the elliptic shape of patterns, both whorls (digits I, II *l.*, III) and loops (digits II *r.*, IV) giving proportions of $\frac{B}{H}$ less than $\frac{2}{3}$. The median proportion of digit V cannot be said to interfere with the elliptic character of the finger-prints of this person, which is marked *E*, 59 (digits III–IV *r.* are shown in Fig. 13 *a–b*).

L. Nr. 10, M. B. A case of very low quantitative values, all patterns being either arches (0–0) or highly reduced loops. The only exception is digit I of the right hand carrying a rather well-developed loop (7–0), while upon the same finger of the left hand we find the highly reduced double loop shown in Fig. 15. The indication of this person is found to be *CT*, 18.

A still lower value is found on the finger-prints of another person in the same table (L. Nr. 3, G. R.), whose indications are *C*, 8·5.

In the line between the two last-named individuals we find L. Nr. 17, A. B., an example of unusually high quantitative value—all patterns being whorls, and most of them also highly developed. They all belong to a broad circular type, one finger (digit I of the left hand) carrying the double loop demonstrated in Fig. 16 *a*. The indications are *CT*, 91.

Finally, in the last vertical line of the table, L. Nr. 7, C. S. gives an example, in which the determination of the pattern-shape does not seem quite simple. Digit I of both hands give a shape-index $\frac{B}{H} > \frac{4}{5}$, in digit II of both hands $\frac{B}{H}$ is between $\frac{2}{3}$ and $\frac{4}{5}$, while upon all other fingers typical ellipses $\left(\frac{B}{H} < \frac{2}{3}\right)$ are found. Such cases are of no rare occurrence; it should, however, here be remembered that the most typical patterns are practically always found upon digit IV, often also upon digits III and V.

Digit I being usually excluded from consideration when determining the pattern-shape of an individual, and the median proportions of digit II not essentially interfering with the highly elliptic shape of all the other fingers, the indications of the individual in question should be *ET*, 69·5.

CHAPTER 6.

Independently Varying Characters of Finger-Patterns.

The three characteristics of the papillary patterns, viz. (1) quantitative value, (2) shape, and (3) twisting tendency, the mutual independence of which was found through the analysis of Chapter 4 (p. 46), have been determined for each of the ten fingers of some 200 individuals. Using the results of such investigation the characteristics of the individuals were noted, as demonstrated in Table XI.

Most of these individuals belong to a series of family-groups, the pedigrees of which are given in Fig. 23 and on Pls. III–IV. Before entering into a discussion of each character separately it might be well

to study in one of these pedigrees (Fig. 23) the way in which not only the characteristics of each individual but also the quantitative values of each separate finger may be noted. When familiar with this method of working, one can from such a pedigree easily reconstruct a rough picture of all the finger-patterns of an individual.

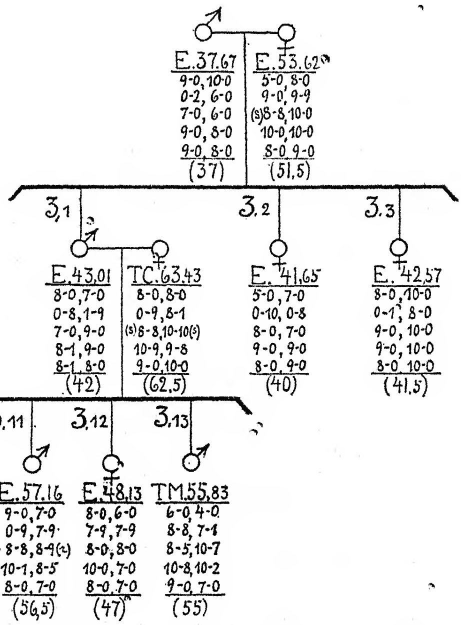


Fig. 23. Pedigree showing the design and quantitative values of finger-patterns of nine individuals belonging to three generations of one family-group (Fam. 3). For explanation see the text and the explanation of Pls. III and IV.

Fig. 23 demonstrates a family-group (Fam. 3) of three consecutive generations. All individuals of the two first generations, that is, parents and three children (3, 1–3, 3) have finger-patterns with an elliptical shape (*E*) and without any twisting tendency. The wife of 3, 1, however, has a circular pattern-shape with twisting tendency (*TC*), which latter appears again, together with a broadening of the pattern-shape (*TM*) in one of her children (3, 13).

The quantitative values of the brother and sisters of second generation (3, 1–3, 3) appear to be strikingly alike, varying between 41·65 and 43·01, all with values coming in between those of the two parents (37·67 and 53·62). Once again, the wife of 3, 1 differs from the fraternity mentioned in having a considerably higher quantitative value (63·43), a trait which

apparently also is carried on to her children, their values having been raised to a range of variation of 48·13–57·16.

As for the patterns of the separate fingers individual 3, 12 may be studied as an example. This girl is, from the figures of the pedigree, seen to have loops on all fingers but digit II, one of the class-values always being 0; these loops are all ulnar, the radial (first) figure being the highest one, and they are all rather well developed, the number of ridges between triradius and core varying between 9–10 (class 6, digit I *l.*) and > 20 (class 10, digit IV *r.*). The elliptical design, finally, characterises these loops as being relatively tall and narrow, their ridges running longitudinally on the finger balls. The second fingers of both right and left hands of the same individual carry well-developed whorls, slightly radial, both having between triradii and centres on the radial side 11–13 ridges (class 7), and on the ulnar 17–20 (class 9). In the same way a reconstruction may be made of the finger-patterns of any individual of our pedigree.

What has been said here about the pedigree of Fig. 23 is valid also for those of Pls. III–IV, the characteristics varying, of course, from one individual to another. These pedigrees and a few others have been used as basis for a study of heredity. They will in the following pages be used, also, as the basis of our discussion about each one of the independently varying characteristics of these patterns.

One technical question ought, however, first to be solved. Below the quantitative values of each individual is, upon all pedigrees, found a figure enclosed in brackets, the value of which is somewhat, but not much, different from the individual values underlined at the top of the individual columns. The figures in brackets below represent the "uncorrected," the underlined figures at the top the "corrected" individual values. The meaning of such distinction will become evident from the following consideration:

The statistics of Chapters 2–3 have shown a very characteristic difference to exist between the various fingers with regard to the distribution of pattern-types upon them. The whorls, that is the pattern-type with the highest quantitative values, are, in all human races investigated, most frequent upon digits I and IV, especially upon these fingers of right hands. The arches, the lowest-valued pattern-type, are on the other side found to have their maximum upon digit II. The loops, finally, representing median quantitative values, are the preponderant patterns of digits V and III. In Chapter 5 we have, further, seen how the *quantitative value of an individual* was supposed to be determined through a simple summation of the values of its ten fingers.

The question now presents itself whether a procedure like the one here mentioned can be considered quite just, no account being taken of the statistical characteristics of the various fingers.

If, for one finger, e.g. digit V, a low value is a statistical characteristic, while another finger, viz. digit IV, is generally found to have patterns of high value, then a relatively high-valued pattern upon digit V would in each special case mean something more than the same pattern found upon a digit IV.

We ought, therefore, certainly before determining the quantitative value of a person, to correct the different finger-values in order to make them really comparable. This has been done in the way shown in Table XII.

In this table the finger-patterns of 125 individuals have been arranged according to their quantitative value, each horizontal line of the table giving one of the ten fingers, while the vertical columns give the different finger-values ranging from 0–10. Each square of the table, therefore, gives the number of patterns occurring upon a certain finger of right or left hand and at the same time showing the special quantitative value of the vertical column to which the square belongs. At the bottom of the table totals are given for right and left hands separately, and for the whole material.

From the material in each horizontal line of the table, the median quantitative values have been determined for each of the ten fingers, for right and left hands, all fingers being taken together, and for the whole material of 1250 fingers. These median values, found in third column from the right side of Table XII, prove the already supposed characteristic difference to exist between the ten fingers, digit II of right hands showing, in our material, a median quantitative value of 4·6, exactly corresponding to that of the sum total of all fingers, while the median values of digits I and IV are seen to be higher, those of digits III and V, as well as of digit II of left hands, to be lower than that of digit II *r*.

Digit II r. has therefore been taken as the unity in relation to which the median values of all other fingers are determined (see last column but one of Table XII). From this finger-relation a factor of correction has been found (last column) with which the value of each finger should be multiplied in order to be comparable with digit II *r*., and therefore also with the corrected values of all other fingers.

For all individuals of the pedigrees each finger-value has been corrected in the way just mentioned before being added for determination

Number of fingers. Dig.	Hand.	0	0,5	1	1,5	2	2,5	3	3,5	4	4,5	5	5,5	6	6,5	7	7,5	8	8,5	9	9,5	10	Number of fingers	Median-values	Finger-relation	Factor of correction
I	r	3	2	3	2	3	5	4	15	18	17	6	1	1	2	2	4	6	9	9	6	7	125	5,35	1,16	0,86
	l	7	1	2	2	5	9	5	17	17	10	9	6	1	2	5	7	4	4	5	4	3	125	4,71	1,02	0,98
II	r	10	8	8	6	2	5	5	4	8	10	5	6	4	5	7	7	8	7	7	2	1	125	4,6	1,00	1,00
	l	9	8	9	5	5	6	9	7	13	6	5	3	4	3	6	4	7	4	8	2	2	125	4,27	0,93	1,08
III	r	7	4	6	7	11	5	9	20	19	10	2	0	0	2	3	2	4	3	6	2	3	125	3,93	0,85	1,17
	l	7	3	6	6	3	8	7	18	22	12	6	3	0	1	2	2	3	5	3	6	2	125	4,20	0,91	1,10
IV	r	0	0	3	4	5	3	5	7	10	21	12	2	1	4	2	8	8	3	12	10	5	125	5,76	1,25	0,80
	l	1	1	4	4	2	2	4	11	12	24	12	2	3	4	6	4	5	10	9	3	2	125	5,34	1,16	0,86
V	r	0	1	2	5	14	6	6	19	20	30	5	3	1	3	2	0	2	3	2	1	0	125	3,68	0,80	1,25
	l	2	0	3	3	6	5	9	28	20	32	10	2	1	0	1	0	1	1	1	0	0	125	4,02	0,87	1,15
I-V	r	20	15	22	24	35	24	29	65	75	88	30	12	7	16	16	21	28	25	36	21	16	625	4,73	1,03	0,97
	l	26	13	24	20	21	30	34	81	84	84	42	16	9	10	20	17	20	24	26	15	9	625	4,47	0,97	1,03
Sum total		46	28	46	44	56	54	63	146	159	172	72	28	16	26	36	38	48	49	62	36	25	1250	4,6	1,00	1,00

TABLE XII. Distribution of quantitative values upon each of the ten fingers, with median values and factors of correction for each finger.

of the individual values[1]. Such corrected values will, as mentioned above, be found underlined at the top; while the uncorrected, reached through a simple addition of the finger-values, have been added in brackets below the class-figures of each individual.

A comparison of the two figures proves the difference between them to be surprisingly small, considering that for each special finger the factors of correction vary from 0·8 (digit IV *r.*) up to 1·25 (digit V *r.*).

The higher values of digits I and IV and the lower ones of digits III and V, in fact, generally balance each other so as to make the effect of their corrections on the individual value less significant.

In the following sections of this chapter each of the independently varying characters of the patterns will be investigated separately, with regard to their general occurrence, as well as with regard to heredity.

(*a*) *Quantitative Value.*

As mentioned above, the quantitative value of individuals, that is, the sum total of the values of their ten papillary patterns, may *à priori* be supposed to vary between 0 and 100, according to the more or less developed state of the patterns.

Experience proves, indeed, that such is the case. Within the family-material individuals are found representing a value not far above 0, others with a value of 90–100, and between these extremes any other value may be found.

It will first be of interest to study the composition of these totals representing the quantitative values of individuals. Are the various patterns of one person usually very uniform with regard to their values, or do high and low values occur irregularly scattered among each other? *May*, in other words, *the quantitative value of an individual be considered a characteristic feature of this individual*, or is it nothing but an accidental expression of independently varying values of the different fingers?

In order to answer this question I have, for 175 individuals, noted the lowest as well as the highest quantitative values occurring upon any of their fingers. The results obtained are shown in Table XIII, where lowest values, combined to groups, are represented in the horizontal lines while corresponding groups of highest values will be found in vertical columns.

The table shows that in 58 individuals, or 33·14 per cent. of the material investigated, the lowest value is 0–1, which means that of an

[1] A table of multiplication for such correction is found at the end of this paper. (Table XXIV.)

arch; no less than 84·4 per cent. of these individuals (49) prove to have also a rather low highest value (0–1 or 2–6), while a few patterns only (9) with their highest value belong to the group of 7–10. In 115 cases the lowest value is 2–6, and in two cases even higher, belonging to the 7–10 group. Of the 115 individuals mentioned 92, or 80 per cent., have their highest value within the highest group (7–10). In other words, out of 58 individuals who carry patterns with the lowest quantitative values nine individuals (15·6 per cent.) only reach at the same time the highest pattern-values; while, on the other side, among 103 individuals with high-valued patterns the same nine individuals, or no more than 8·8 per cent., are found with patterns also of the lowest values.

		Highest value				
		0–1	2–6	7–10	Sum total abs.	%
Lowest value	0–1	$\underbrace{3 \quad 46}_{84,4\%}$		9	58	33,14
	2–6		23	92 (91,2%)	115	65,7
	7–10			2	2	1,16
		3	69	103	175	100

TABLE XIII. Range of variation of quantitative values.

It seems evident, from this table, that there exists some coincidence between the quantitative values of the various fingers of one and the same individual, the patterns representing either relatively low, or relatively high values. The individual values may, therefore, *be considered as characteristic of the individual itself* not only as the sum of the varying finger-values.

This result agrees very well with that reached with regard to the correction of quantitative values. The finger-values of each individual seem in fact to be varying within a certain range and round a median value, both of which are characteristic of the individual.

This peculiar balancing of high- and low-valued patterns of one and the same individual is demonstrated also through a comparison of *variation curves of finger-pattern values* with the corresponding curve of *individual pattern-values*. A study of these curves gives at the same time other results of interest.

The curves of Figs. 24 and 25, showing the variation of pattern-values

of separate fingers are based upon the material already studied in Table XII, that is, the fingers of 125 individuals.

The curves of Fig. 24 correspond to the three bottom lines of that table, giving the total of all 1250 fingers of both hands as well as those of right and left hands separately.

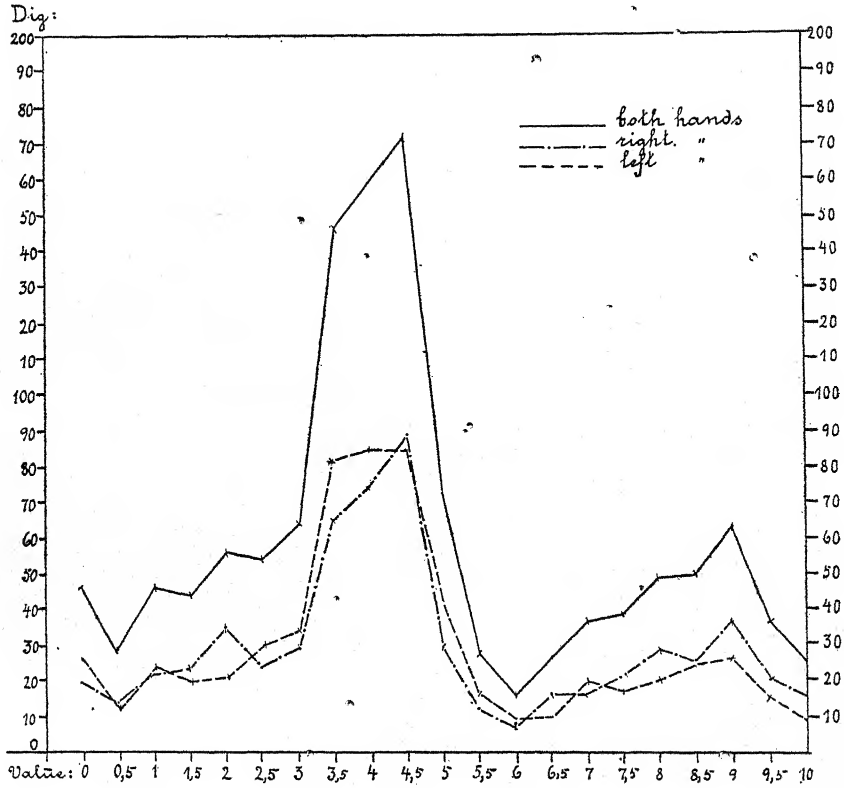


Fig. 24. Variation curves of pattern-values of the fingers of both hands, 1250 fingers, and of right and left hands separately, 625 fingers.

The three curves all show great maxima at the values of 3·5–4·5, while in each curve a considerable maximum is found also at the value of 8–9. A comparison of the right- and left-hand curves proves the maxima mentioned to be somewhat more accentuated in the fingers of right hands than in those of lefts.

In Fig. 25 each curve is based upon 250 fingers, no distinction here having been made between right and left hands. These curves clearly illustrate the differences between the various digits.

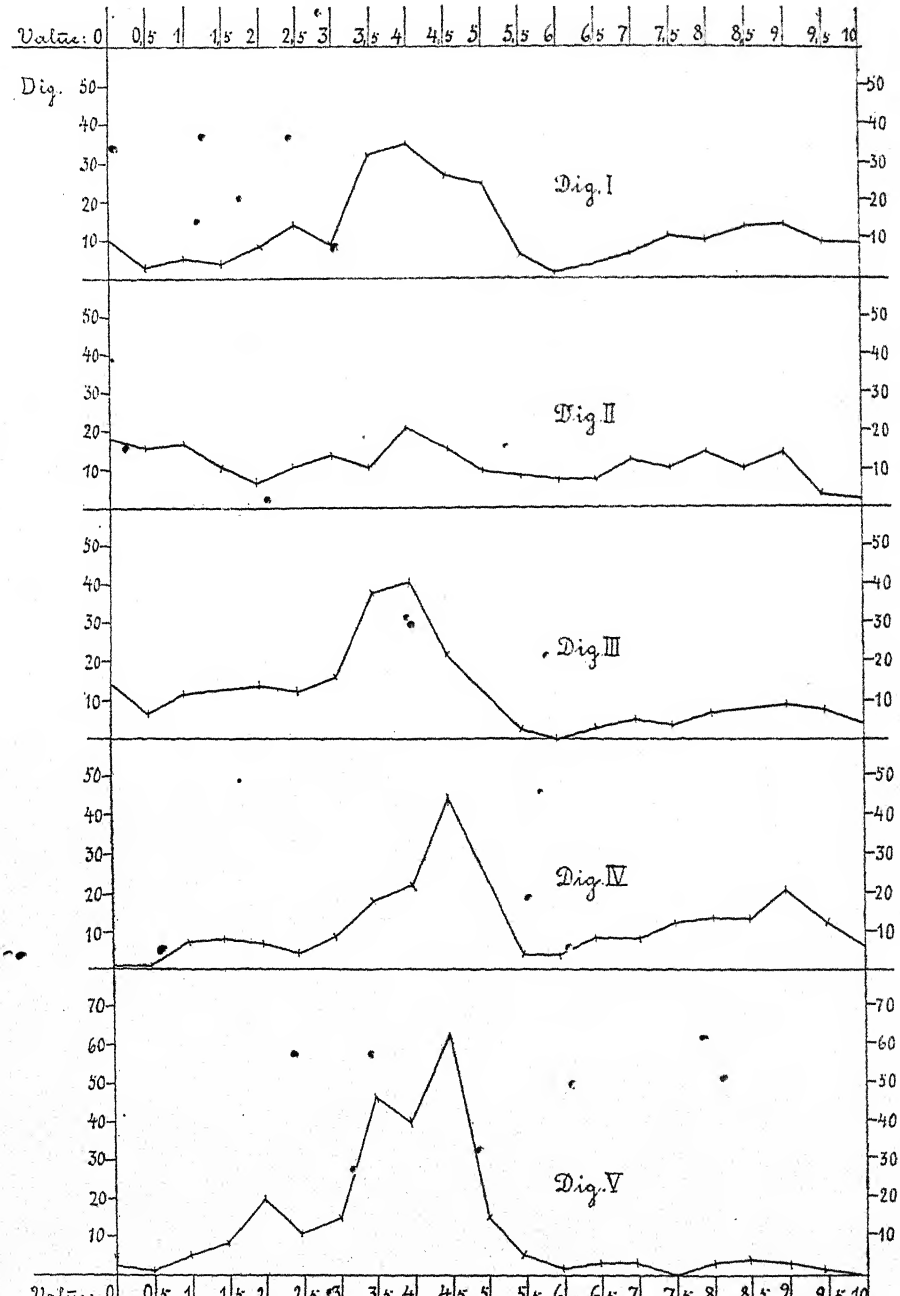


Fig. 25. Variation curves of pattern-values of digits I–V separately, each curve 250 fingers.

The highest maximum of the summation curve (Fig. 24), that above the value of 3·5–4·5, is found also in each of the finger-curves, but very differently developed. Digit V is with regard to this maximum far in advance of the other fingers, then follow digits IV, III and I close up to each other, while digit II keeps so far behind that the maximum would here scarcely be noticed without comparison with the other fingers.

The lower maximum (Fig. 24, above the values of 8–9) is clearly visible in the curve of digit IV and may be seen also in that of digit I, while in digits III and V the slight rise at this place would scarcely be called a maximum; the curve of digit II is in its whole length remarkably even and scarcely any point can be reckoned as a maximum.

The five finger-curves differ remarkably also with regard to the lowest values (0–1), such values being scarcely represented among fourth and fifth fingers, somewhat more in digits I and III, their occurrence reaching its maximal height in digit II.

These results with regard to the quantitative values of digits I–V agree perfectly well with the results of general statistics of the three common pattern-types—whorls, loops and arches (Tables I–II).

The most common type was found to be the loop, which, according to our classification, represents (in unreduced state) the quantitative values of 3·5–5. The highest maximum, therefore, of the curve of Fig. 24 is doubtless caused by the very frequent occurrence of this pattern. With this view the five curves of Fig. 25 all agree, the loop-maximum being highest in the curve of digit V, and scarcely visible in that of digit II, just what was to be expected from the statistical occurrence of the loop pattern upon the various fingers.

The second maximum of the summation curve (Fig. 24) at the values of 8–9 corresponds in the same way to the occurrence of more or less unreduced whorls, the quantitative value of such patterns varying from 8–10. Remembering that whorls occur most frequently upon digits I and IV of right hands (Tables I and II) we understand also why the right hand curve of Fig. 24 at this point shows a considerably higher maximum than that of left hands, as well as why this second maximum is visible especially in the curves of digits IV and I.

For the lowest values, those of arches, the summation curve of Fig. 24 shows a rather conspicuous rise, which, as seen in Fig. 25, is caused by their relatively very frequent occurrence among the patterns of digit II, partly also those of digit III, the same two fingers where, according to the general statistics of Tables I and II, arches were to be expected.

So far a full agreement exists between the statistical occurrence

of pattern-types on one side, and the grouping of patterns according to their quantitative values on the other side.

Through the consideration especially of the summation curve one important question arises with regard to the natural connection between different pattern-types, or, in other words, between different quantitative values. *Does the series of falling values from 10 to 0 represent also a continuous series of stages connecting the high-valued patterns, the whorls, through those of the median values, the loops, with the lowest values, the arches?* A series like this would fully correspond to the phylogenetic view maintained by Whipple and other authors (see above, p. 24) and is strongly supported by a comparison of different papillary patterns. We have thus seen (Figs. 4 and 5, 10–17) many examples of a gradual transition from all sorts of whorls into loops, and from loops into arches, as well as transitions directly between whorls and arches. Is this view supported also by the curves just demonstrated?

The answer to this question is negative. If all loops as well as arches have arisen through a gradual reduction of whorls, we should expect to find also a gradual transition in the occurrence of the various reduction stages. The high maximum of the summation curve (Fig. 24) formed by the loops, therefore, seems to indicate that such patterns, besides representing whorls checked in their development, also have an origin and existence of their own. As mentioned in a previous chapter (p. 26), Schlaginhaufen (1906) has, from his results upon Primate-plantae, already suggested that such may be the case, saying (p. 679): "Jedoch ist es denkbar, das die menschlichen Simus obliqui curvati und verwandte Formen direkt aus entsprechenden Figurae tensae hervorgegangen sind ohne den Weg ihrer Entwicklung durch die geschlossenen Fig. curvatae genommen zu haben."

The results of our investigations give a strong support to this suggestion of Schlaginhaufen.

From a comparison of certain pattern-series (Figs. 10, 14, 16, 17) it seems evident that loops may occur which should beyond doubt be considered as whorls checked in their development. But at the same time the statistics prove the frequency of large loops to exceed by far the occurrence to be expected by such a reduction stage. An attentive study of the various loops indicates also a difference between them pointing to a double origin, many large loops especially often found upon digits III and V (Fig. 11 *a*) being, indeed, too fully and too harmoniously developed to represent transition stages only.

It seems to me, therefore, more correct to consider both whorls and

large loops as fully developed (original?) patterns upon human fingers, from both of which a transition may occur into patterns of a lower quantitative value, arches being the end-result of such transition and loops often occurring also as a transitional stage during the reduction from whorls into arches.

In order to test this hypothesis statistically all patterns with two triradii, therefore obviously derived from whorls, have in the curves of Figs. 26 and 27 been separated from those with only one triradius, the latter group containing, besides all patterns derived from original loops, also such lower valued patterns representing or derived from transitional

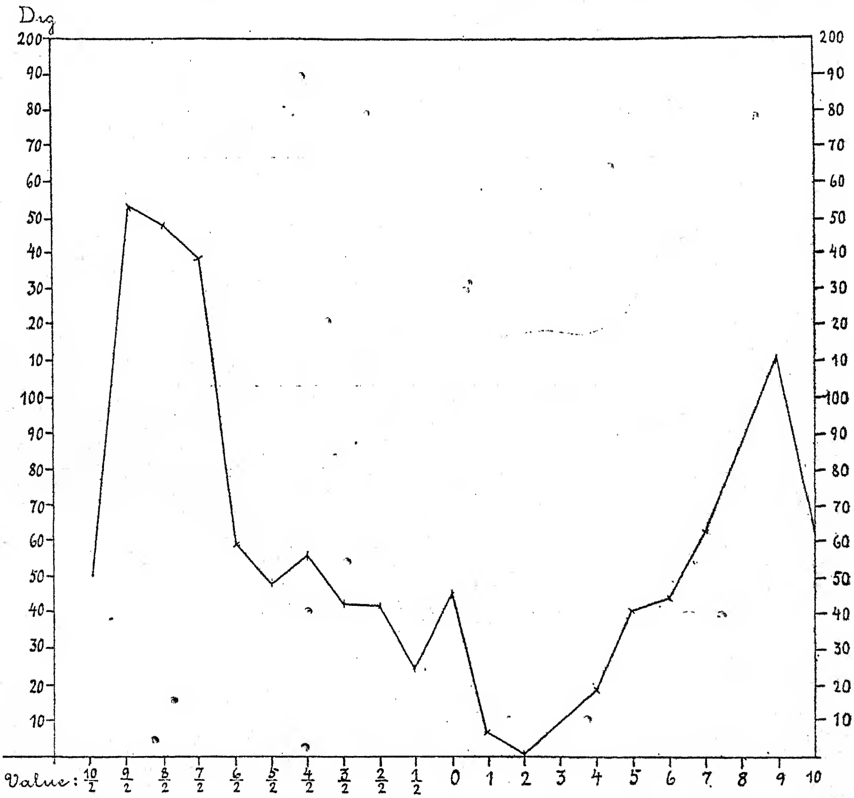


Fig. 26. Variation curve (cf. Fig. 24), in which all patterns with two triradii (values 0–10) are placed to the right, those with only one triradius (value $\frac{1}{2}$–$\frac{10}{2}$) to the left side of the 0-point.

loops. The lower values, therefore, will in great abundance be found upon the loop side of the curves.

In all these curves of Figs. 26 and 27 the patterns with two triradii

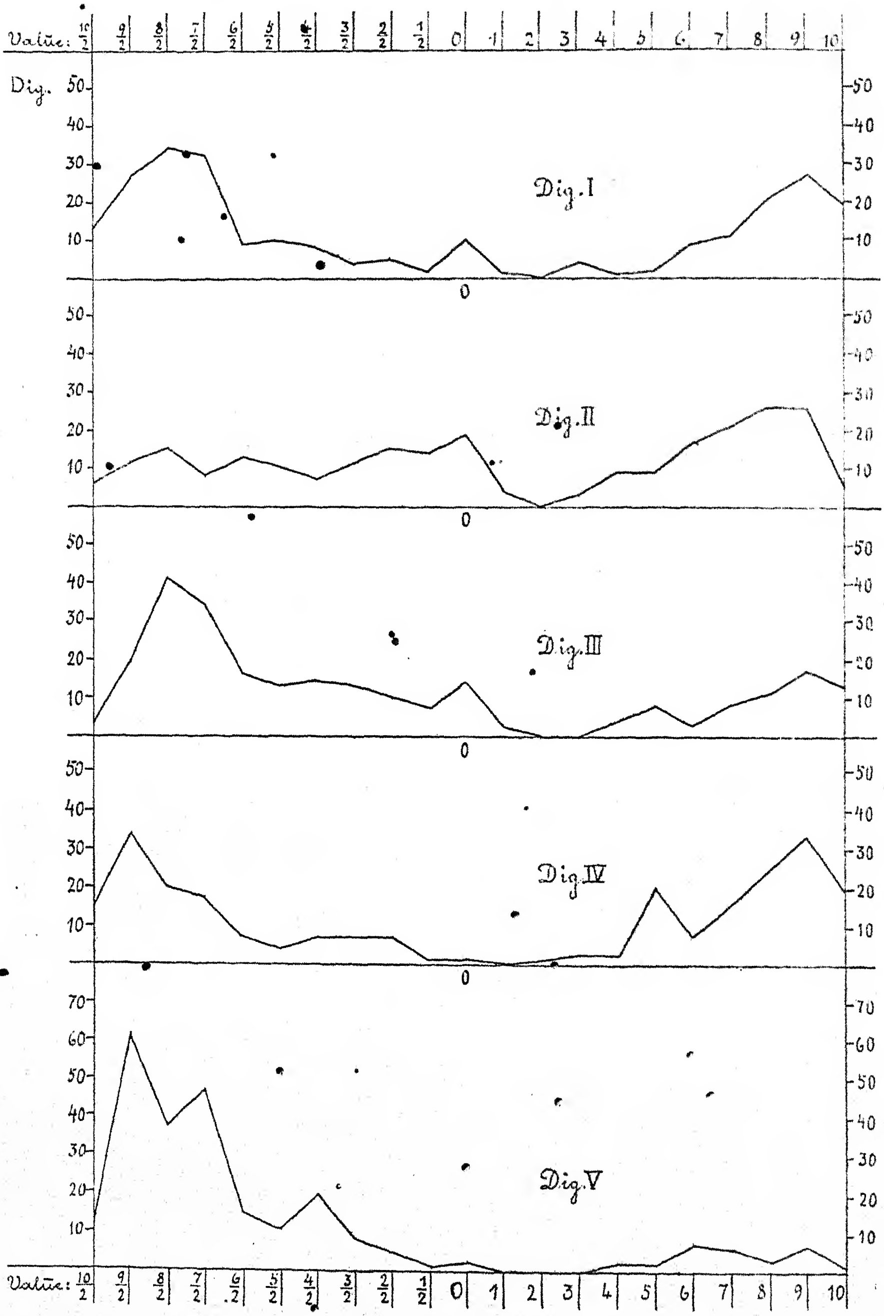


Fig. 27. Curves of separate fingers (cf. Fig. 26).

are found on the right side of the figure, and the values 0–10 here means, as usual, the averaged value of both sides of the pattern. The left side of each curve consists of all patterns with only one triradius. The deltaless side of each pattern carrying the values 0, the figures $\frac{1}{2}$–$\frac{10}{2}$ of the curves will, therefore, also here give the average values of both sides of the pattern.

The summation curve, Fig. 26, gives an interesting picture. Upon each side we find a maximum of the fully developed patterns, the unreduced whorl (value 8–10) to the right, and the unreduced loop (value $\frac{7}{2}$–$\frac{10}{2}$) to the left, the number of loops being by far the greater.

The slope of the curve towards the 0-point is very much steeper on the whorl side, which means that a transition from whorls directly into arches is rather rare, the arches commonly being reached through a transitional loop-stage. The rise of the curve at the 0-point is obviously caused by the fact that arches no longer represent a transition-stage, but rather a stage of accumulation of the most reduced patterns.

The five curves of Fig. 27 give further illustrations of the relation between whorls and loops, each one of the fingers here being taken into consideration separately.

The most remarkable feature of these curves, as in those of Fig. 25, is perhaps their great difference with regard to the 0-point, patterns of the lowest values being scarcely represented in digits IV and V, while in digit II this point represents a maximum of the curve.

The loop side of the curve of digit II contains only few unreduced patterns, but a continuous series of reduction stages, augmenting towards the lower values. In digit III also the number of reduced loops is rather high at all stages, but here, as well as in all the other fingers, there exists also a well-defined maximum of high-valued loops. Such is the case especially with digit V, in which the unreduced loops play a very great part, while reduced loops as well as whorls and arches are very sparely represented.

The highest maximum of unreduced whorls is found in the curve of digit IV, the reduction of whorls upon this finger apparently stopping at a value of about 5, while very few patterns on either side of the curve of this finger reach the arch-value. Also upon digits I and II whorls are rather frequent but here in a relatively more reduced shape. While, therefore, the total number of whorls is very similar upon the first finger and the fourth, the fall of the curve of digit I is considerably more slow and gradual than in that of digit IV.

The above results with regard to the *double nature of loops* were

reached at an advanced stage of my investigation, and have, therefore, not been taken into consideration as influencing the basis of our classification. A further study of the loops will be necessary before this question can be definitely solved. It should be remembered, however, that in the present paper, for the reason mentioned, some uncertainty prevails with regard to the classification of large loops, the fully-developed "original" loops probably belonging to higher classes (6 or 7) than the ones (classes 4 and 5) to which they have been referred. This would, with reference to the curves of Fig. 24, mean that the high maximum above the values 4 and 5 should, at the sacrifice of its height, be extended towards the right side to the values of classes 6 and 7.

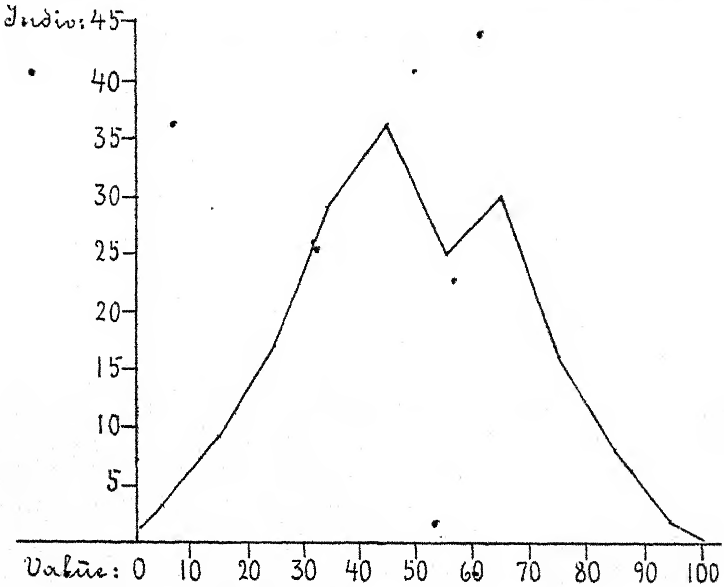


Fig. 28. Variation curve of individual pattern-values, based upon investigation of 175 individuals.

We now turn to the corresponding *curve of variation of the individual pattern-values,* based upon a material of 175 persons mostly belonging to the family-groups of this paper (Fig. 28).

Compared with the very irregular curve of Fig. 24 this individual curve seems surprisingly smooth and regular. Also here we have, it is true, an irregularity at the top of the curve, this top being double. But the two maxima thus indicated are not nearly so distinct, nor so deeply separated as in the curve of finger-values. Taking into consideration what has just been said about the classification of large loops, the

summit of the curve, that above 40–50, ought probably to be moved towards the right side, that is, the gap between both maxima would be filled up more or less, and the individual curve would become approximately symmetrical.

Such a comparison between the pattern-value curves of separate fingers and that of individuals strongly supports the assumption already made (p. 60) of the varying finger-values being, as it were, controlled by the pattern-value of the individual, so that high- and low-valued patterns occur upon the ten fingers within a range of variation characteristic of the individual in question. In variation curves based upon separate fingers (Figs. 24 and 25) all such oscillations will be of full effect, while in the individual curve (Fig. 28) they cancel each other and disappear from the picture which now gives only median values characteristic of each individual.

When speaking about these oscillations of pattern-values from finger to finger in one and the same individual, it seems natural to recall the causal connection which no doubt exists between the configurations of papillary patterns and the shape and elevation of each special finger-ball (see Chapter 3, p. 26).

It is impossible at the present stage of our knowledge to decide the exact nature of the relations existing between balls and patterns. It is very probable, however, that the papillary patterns with varying details of their configurations may also be considered as indicators of changes in the shape of the finger-balls, too delicate to be directly observed. For a discussion of heredity it is, therefore, impossible in each case to decide whether the genotype in question determines the configuration of the pattern directly, or only indirectly through the shape of the finger-ball.

With regard to the quantitative values of finger-patterns it seems to me very probable that they to some extent depend on the finger-balls, such dependency causing the oscillations just studied round a median value characteristic of the individual. One and the same hereditary pattern-design might, thus, upon one finger, e.g. digit IV, develop into a whorl, while on digit V it appears as a loop, and on digit II perhaps even as a simple arch, all these differences being due to the characteristic elevation and shape of each finger.

For the question of heredity, therefore, the oscillating finger-values are of little importance in comparison with the median value of the individual, the inheritance of which should, therefore, before all, be investigated.

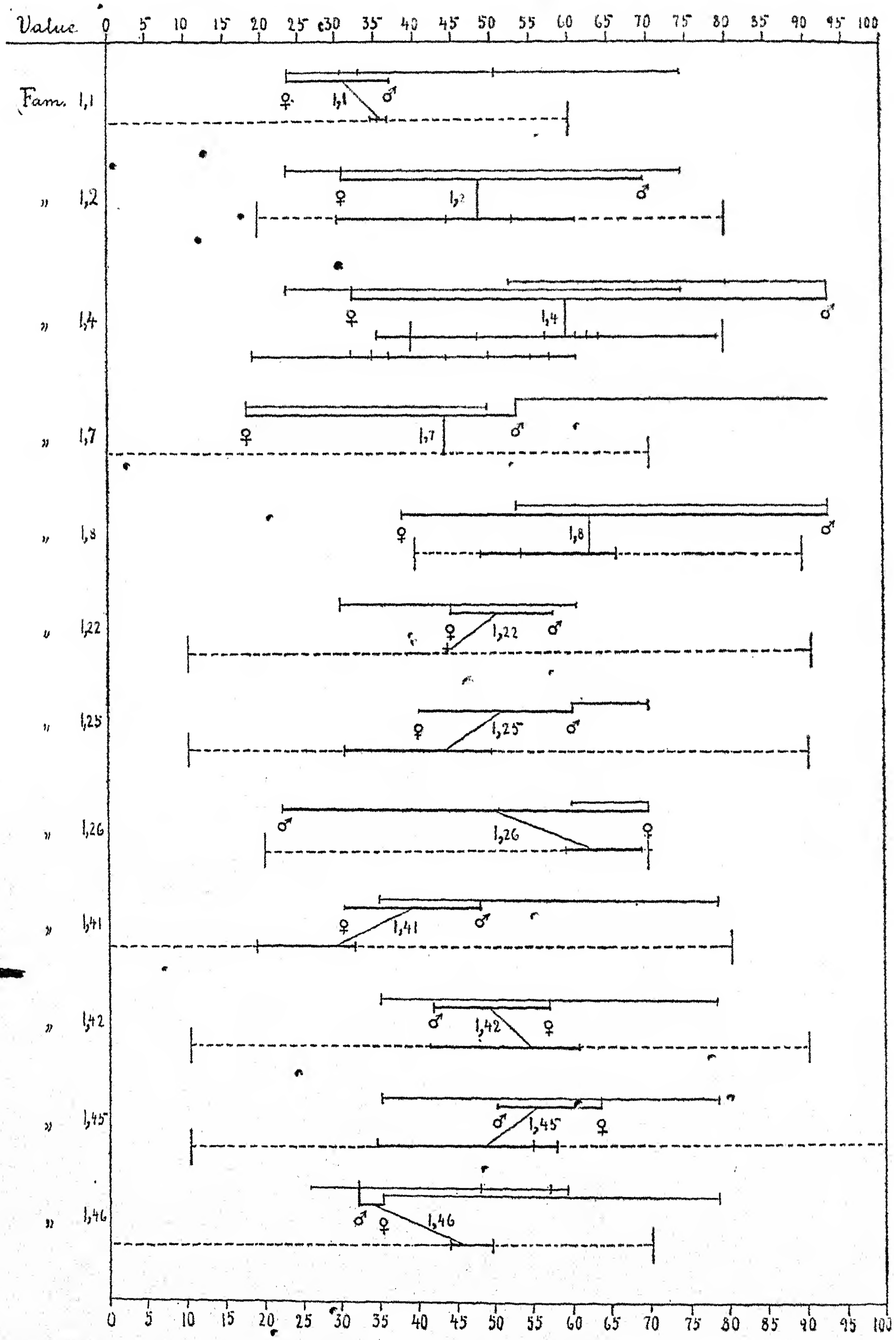


Fig. 29 *a*.

Fig. 29 *a–b*. The families of Fig. 23 and Pls. III and IV graphically represented, according to the quantitative values of parents and children. Explanation in the text. Broken lines show the "expected" range of variation based upon the supposition of five pairs of multiple factors determining the quantitative value of individuals.

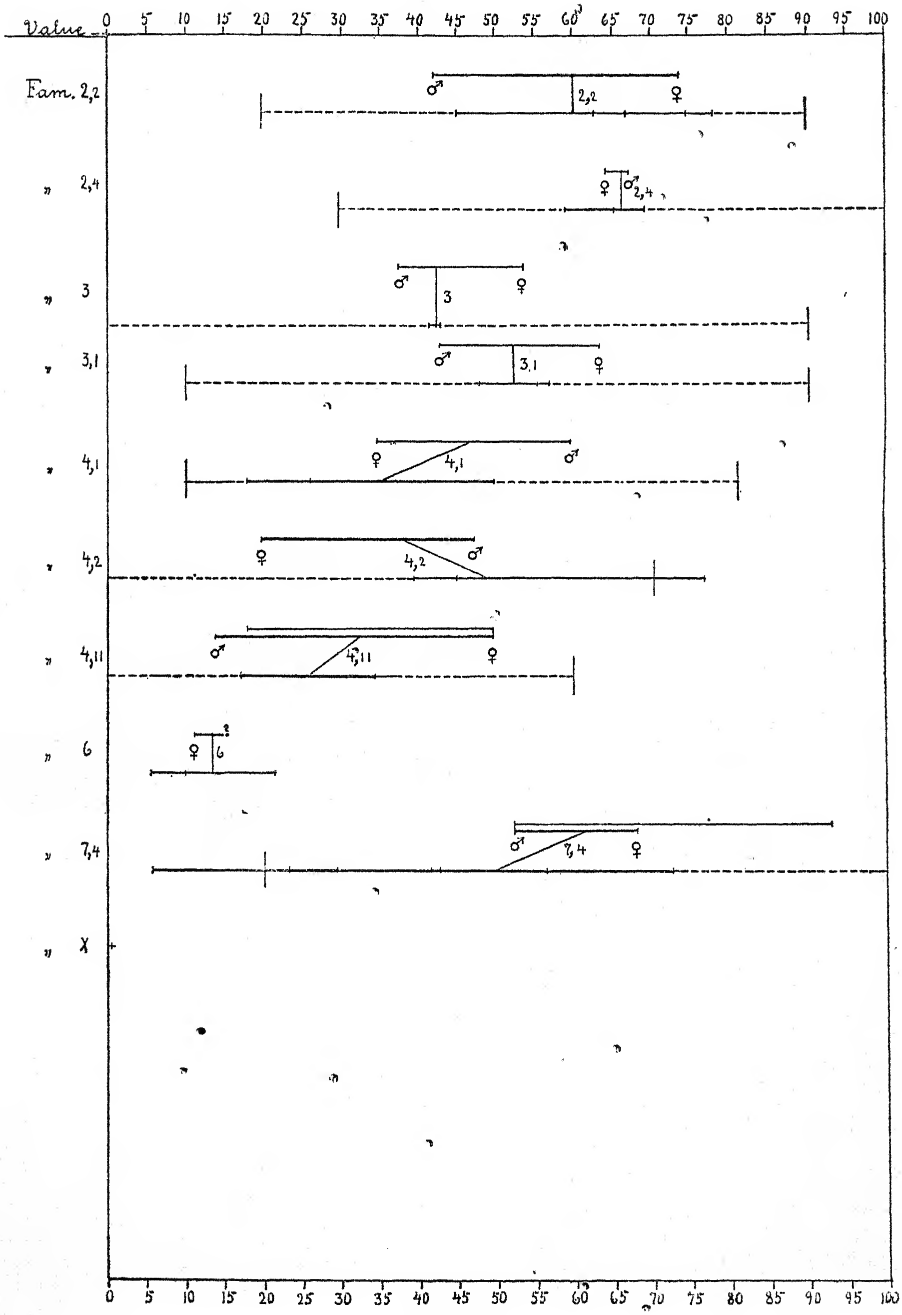

Value
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100
Fam. 2,2
♂ 2,2 ♀
" 2,4
♀ ♂ 2,4
" 3
♂ 3 ♀
" 3,1
♂ 3,1 ♀
" 4,1
♀ 4,1 ♂
" 4,2
♀ 4,2 ♂
" 4,11
♂ 4,11 ♀
" 6
♀ 6 ?
" 7,4
♂ 7,4 ♀
" X
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100

Fig. 29 *b*.

Taking as a starting-point the approximately symmetrical variation curve of such values (Fig. 28) we have before us the picture of a fluctuating variation, or, *this curve might also represent the varying phenotypes of an hereditary character, due to multiple factors.*

In order to test this possibility the family-material of Fig. 23 and Pls. III and IV has been arranged graphically, according to the quantitative values of the individuals, as seen in Fig. 29 *a b*.

In these schemes the various families are represented by horizontal lines, each line meaning one generation, and each individual being noted at a place on the horizontal line corresponding to the individual value of their finger-patterns. In a number of cases the range of variation of the parental "fraternities" is demonstrated by thin horizontal lines above, and connected with either father or mother. In one case (Fam. 1, 4), the third generation, the grandchildren are also represented by a line below that of the children.

In most of the families thus illustrated we find the pattern-values of the children within the range of the line representing the values of their parents, the filial values being as a rule rather equally distributed along the line of their generation. Typical examples of such distribution are the Families 1, 2; 1, 4; 1, 7; 1, 8; 1, 22; 1, 42; 2, 2; 3; 3, 1; 4, 11. In other cases, as Fams. 1, 1; 1, 26; 1, 45; 1, 46, in which the distribution of filial values might seem aberrant, the hereditary nature of the character becomes more probable when the fraternity lines of one or both parents are observed. Fam. 2, 4, in which the values of both parents are very closely related, the range of their fraternity values not being known, may find its explanation in the same way as e.g. Fam. 1, 46, the picture of which is rather similar.

Of genetical importance are the two incomplete families, Fam. 6 and Fam. X, in which one or both parents are wanting but where all investigated members of the families have strikingly low pattern-values. Statistically such low values are very rare, and their coincident occurrence in two or more members of the same family can be explained only through the suggestion of heredity.

As already mentioned, the shape of the variation curve approximating that of the normal curve would, on the supposition that the quantitative value of finger-patterns is an hereditary character, indicate that it is based upon a series of multiple factors. This assumption is supported also by the very regular distribution so often found for the quantitative value of the children round and between the values of both parents.

Looking upon each single fraternity, as well as the whole population investigated, as an F_2 generation—the parents of each fraternity being without doubt in an overwhelming number heterozygotes—we should expect to find at one end of the curve a relatively small number of recessive homozygotes with a value of their finger-patterns like 0, and at the other end a correspondingly small number of high-valued dominant homozygotes with a value of 100, while between these points all individuals are supposed to be either heterozygotes with regard to one or more of the multiple factors responsible for the quantitative development of finger-patterns, or homozygous, but with some factors recessive and others dominant.

Through a determination of the number of recessive or dominant homozygotes in a sufficiently large F_2 generation we should have an indication of the number of hereditary factors concerned.

Of course, no human fraternity exists in any way large enough for such use. A scientifically based solution of this question is, therefore, excluded.

It would, however, be of great interest to test further our working hypothesis, and especially to find whether the apparently aberrant families of Fig. 29, e.g. Fams. 1,46; 2,4; 4,2; 7,4, etc. in which the quantitative values of the children differ more or less obviously from those of the parents, constitute objections to our assumption of multiple factors. I have, therefore, made use of the fact that the numerical distribution of phenotypes within an F_2 generation following this mode of inheritance is the same as that of an accidentally composed population, trying to find the number of individuals carrying the lowest and highest quantitative pattern-values in a population large enough to give reliable results.

A population suitable for this purpose was found in the large and excellently arranged material of the Court of Justice of Kristiania (24,518 individuals), already used for the general statistics of finger-patterns (Tables I and II).

The statistical occurrence of pattern-types within this population corresponds very well with that of the smaller one, represented in our family material. Like the latter it would, therefore, if arranged according to the quantitative values of each pattern, doubtless also form a symmetrical curve of variation.

In this material I have determined the number of individuals with a pattern-value of 0, that is with simple arches on all ten fingers, as well as those with a value of 100, unreduced whorls on all fingers.

The numbers obtained were 26 individuals with a value of 0, and 28–30 with a value of 100, the determination of arches being absolutely certain, while that of the whorls was questionable in a few cases. Twenty-six individuals in a population of 24,518 means 1 : 943, which approximates 1 : 1024 closely enough to indicate that five pairs of multiple factors might be cumulating their effects in determining the quantitative value of papillary patterns upon human fingers, either directly or through a detailed modelling of the finger-balls upon which the patterns are developing.

According to this hypothesis the value of 100 might be expressed by the formula *AABBCCDDEE*, while that of 0 would be *aabbccddee*, all intermediate values showing genotypes with the same factors partly dominant and partly recessive. Assuming that the effects of these ten factors are equal and cumulative we may make also the further assumption that each dominant factor, as compared with its recessive allelomorph, augments the pattern value of an individual with ten units. We should, then, expect to find a series of phenotypes distributed like that of the coefficients of the expanded binomial $(a + b)^{10}$, that is:

Value	0	10	20	30	40	50	60	70	80	90	100
No. of indiv.	1	10	45	120	210	252	210	120	45	10	1 = 1024

Through reduction of this series to a sum total of 175 individuals, corresponding to the number of individuals whose quantitative values are represented in the curve of Fig. 28, we get the (expected) series of Table XIV, while the observed series basing the curve mentioned is added below for a comparison.

The two curves of these series are shown in Fig. 30.

Value:	0	10	20	30	40	50	60	70	80	90	100
Expected:	0·2	1·7	7·7	20·5	35·9	43·0	35·9	20·5	7·7	1·7	0·2
Observed:		3	9	17	29	36	25	30	16	8	2 = 175

TABLE XIV. "Expected" and "observed" series of variation of the quantitative values of 175 individuals.

As will be seen from both table and curves the general conformity of the two series is somewhat disturbed with regard to the extreme values on both sides as well as at the top of the curve.

The difference between both curves with regard to their top is, however, not surprising, the broken line of our empirical curve being, as discussed above, apparently due to the difficulties of a correct classification of the large loops (cf. p. 68).

The other deviation, consisting in a surplus in the frequency of extreme individuals, is also easily explained. Our material is, namely, in so far not representative, as during my investigation I have been especially interested in low- and high-value families, hoping to find there an example of the homozygous conditions.

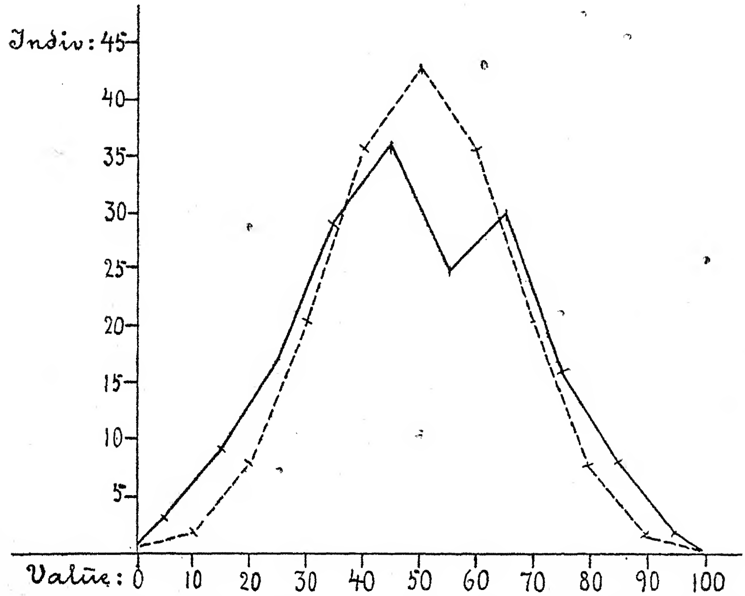


Fig. 30. The curve of Fig. 28, representing the pattern-values of 175 individuals, as compared with the binomial curve (see Table XIV).

These facts remembered, the conformity of the two curves seems, indeed, sufficient for maintaining, *as a working hypothesis*, the supposition of five pairs of multiple factors causing the individual pattern-values.

It remains, however, still to see how such a suggestion will work in each special case of observed family results.

As a representative family we may first look at Fam. 1, 4 (Fig. 29 *a*), with its great difference between the pattern-values of both parents (♂ 92·96, ♀ 32·37), and with no less than eight children, all investigated.

The father of Fam. 1, 4 with his extraordinarily high pattern-value of 92·96 should, according to our working hypothesis, have nine dominant representatives of the multiple factors in question. His genotype, therefore, may be expressed as *AABBCCDDEe*, while that of the mother (value 32·37) might be *AaBbCcddee* (Table XV). The germ-cells of the father would, with regard to the pattern-factors, be of two

kinds only, namely *ABCDE* and *ABCDe*, while those of the mother would, with a trihybrid genotype, represent eight different combinations of pattern-factors. (The three dominant factors of the mother might, of course, occur in any of the five pairs of allelomorphs, as, e.g., *AABbccddee* or *aaBbccDDee*. A distribution of them upon three different pairs (making the genotype trihybrid) is, however, the condition necessary for a maximal variation of the germ-cells.) As shown in Table XV crossings between such germ-cells would result in 16 combinations of factors, the

	Germ-cells of mother.							
Germ-cells of father	ABC de	ABc de	AbC de	aBC de	Abc de	aBc de	abC de	abc de
ABCDE	8	7	7	7	6	6	6	5
ABCDe	7	6	6	6	5	5	5	4

TABLE XV. Number of dominants in fertilized eggs. Range of variation of quantitative values of Fam. 1, 4.

number of dominants of which would vary between 4 and 8, representing finger values of 40–80, with a frequency of each value corresponding to the series 1–4–6–4–1. Our expectations are, as will be seen (Fig. 29 *a*), in this case fully realised in so far as among the eight children all groups of values are represented, the median value being the one with the highest frequency.

All other families might be treated in the same way. For our purpose it will, however, be sufficient to determine for each family the expected range of variation of the pattern-value in order to compare this result with the values observed in an investigation of the children.

The results of this investigation are shown in Table XVI. The expected range of variation of a family will depend upon the number and distribution of dominants among the multiple factors in question in the genotype of both father and mother, and especially upon the maximal and minimal numbers of dominants in their germ-cells. A cross between germ-cells of minimal value will give the lower border of the range of variation, while its upper border will be reached through crosses between germ-cells with maximal values.

A comparison between the expected variation and that observed shows as a general rule the pattern-values of all investigated children falling within the expected range, even where the average values of

	Parents			Children		
Fam.	Pattern-value	Dominants		Range of variation		Number
		Som.	Germ-cells	expected	observed	
1,1	37 36 23 64	4 2	0 – 4 0 – 2	0 – 60	30 – 40	3
1,2	69 52 30 90	7 3	2 – 5 0 – 3	20 – 80	30 – 60	4
1,4	92 96 32 37	9 3	4 – 5 0 – 3	40 – 80	40 – 80	8
1,7	53 42 18 30	5 2	0 – 5 0 – 2	0 – 70	40	1
1,8	92 68 38 20	9 4	4 – 5 0 – 4	40 – 90	50 – 70	3
1,22	57,71 44,58	6 4	1 – 5 0 – 4	10 – 90	40	1
1,25	60,08 40 52	6 4	1 – 5 0 – 4	10 – 90	30 – 50	3
1,26	22 78 69 92	2 7	0 – 2 2 – 5	20 – 70	60 – 70	2
1,41	48 30 30 91	5 3	0 – 5 0 – 3	0 – 80	20 – 30	2
1,42	42 31 57 05	4 6	0 – 4 1 – 5	10 – 90	40 – 60	2
1,45	50 50 63 75	5 6	0 – 5 1 – 5	10 – 100	30 – 60	3
1,46	32 46 35 46	3 4	0 – 3 0 – 4	0 – 70	40 – 50	2
2,2	42 18 74 04	4 7	0 – 4 2 – 5	20 – 90	40 – 80	5
2,4	67 39 64 60	7 6	2 – 5 1 – 5	30 – 100	60 – 70	3
3,0	37 67 53 62	4 5	0 – 4 0 – 5	0 – 90	40 – 50	3
3,1	43 00 63 43	4 6	0 – 4 1 – 5	10 – 90	50 – 60	3
4,1	60 (?) 34 90	6 3	1 – 5 0 – 3	10 – 80	20 – 50	3
4,2	47 24 19 92	5 2	0 – 5 0 – 2	0 – 70	40 – 80 (77)	3
4,11	13 98 49 89	1 5	0 – 1 0 – 5	0 – 60	20 – 30	2
7,4	52 41 68 34	5 7	0 – 5 2 – 5	20 – 100	10 – 70 (6)	7

TABLE XVI. Range of variation of quantitative values within all families of Fig. 29 *a–b*.

parents and children (Fams. 1, 41; 1, 46) would seem to indicate a considerable deviation. In each family of Fig. 29 *a–b* the expected range of variation is shown by a broken line.

There are, indeed, only two exceptions to this rule, namely, the Fams. 4, 2 and 7, 4. In the first-named family the expected range of variation of the pattern-value is from 0 to 70, while the value of one of the children reaches beyond this range to 77. Admitting, however, the probability of fluctuating variation within each genotype, this difference should perhaps not be considered large enough to represent a real exception to the rule. In the other family (7, 4) the difference is found on the lower border of the expected range of variation, and here it is so large —6 instead of 20—that it can scarcely be explained as an effect of fluctuation.

Some mutational change within one of the seven dominant allelomorphs of the mother, making it lose its dominance, would in this case produce the effect observed in one of the children; it may, however, also have been produced through a change in the effect of some "modifying" factor or factor-groups.

From the above discussion I feel justified in suggesting that *the quantitative pattern-value of individuals may be due to the effect of multiple factors* (five pairs?), influencing either the finger-patterns directly or, more probably, the shape of the finger-balls, which again form the base of development of the papillary patterns. The effects of these multiple factors are not equally developed upon all ten fingers, each of these having its own characteristics distinctly exhibited statistically.

(*b*) *Design of finger-patterns.*

(*α*) *Pattern-shape, circular-elliptic.*

As shown in Chapter 4 there is a very considerable difference between the patterns with regard to their shape, some of them being narrow elliptical while most are broad and approximately circular. Between these two extremes we find also a median type of shape. Such distinction may be made not only for whorls but also for loops and arches, the methods of classification having been demonstrated above (Chapter 5, Pls. I and II). In the pedigrees (Fig. 23 and Pls. III and IV) the pattern-shape of each individual is marked as *E* (elliptical), *M* (median) or *C* (circular).

An investigation of these pedigrees will soon convince one of the

heredity of this character. In the large Fam. 1, for example (Pl. III), the typical pattern-shape is circular, no *E* occurring in this family except where it is brought in from outside. This is the case in the family branch 1, 2, where a woman with *M* is married to a man with elliptical shape of his patterns. Within this branch the ellipse appears not only in three of the children but also in the third generation (1, 211).

A very different picture is given by the two families 2 (Pl. IV) and 3 (Fig. 23), both typical ellipse families. In Fam. 2 the old grandmother was found to have a narrow elliptical pattern-shape, the same being the case also with her three children investigated. One of these (2, 2), herself elliptical, married a man with circular patterns, among the children were three elliptical and two median ones; another daughter (2, 4), whose husband had circular patterns, has also three children all with ellipses. Ellipses are also found in both parents of Fam. 3 as well as in all children investigated; one of these children, a son (3, 1), is married to a woman with broad circular patterns, and among their children two have elliptical, the third one a median pattern-shape.

In Table XVII all families of our pedigrees are arranged according to the pattern-shapes of both parents. Here we find, in the median column, four matings, with 12 children in all, in which one parent has circular (*C*), the other elliptical (*E*) patterns. One only of these children shows a clearly circular pattern-shape, while in eight it is elliptical, and in three median. This might indicate a dominance of *E* over *C*, a suggestion which is supported also by the results of the 11 (or perhaps even 13[1]) crossings shown in the two first columns of the same table, in which none of the parents have an elliptical pattern-shape. Among the 35 (or 41?) children of these matings no single one appeared to have elliptical finger-patterns, just the result to be expected if *C* was the recessive character.

In the two columns at the right side of the table we find five (perhaps six?) matings between persons, none of whom have circular pattern-shapes. If *E* is considered the dominant character of a monohybrid crossing, we should here expect among the 14 (17?) children to find a few also with a recessive, circular pattern-shape. This is however not the case, and these latter crossings, therefore, do not give support to the supposition of *E* being the dominant factor. The number of matings, as well as that of children, is, however, especially in these two columns, so small that no decisive weight should be attached to the results here given.

[1] In the questionable families at the bottom of first and last columns of Table XVII only one of the parents has been investigated.

Parents: C × C					Parents: C × M					Parents: C × E					Parents: M × E					Parents: E × E				
Fam.	Children C.	M.	E.	Sum	Fam.	Children C.	M.	E.	Sum	Fam.	Children C.	M.	E.	Sum	Fam.	Children C.	M.	E.	Sum	Fam.	Children C.	M.	E.	Sum
1,4	8	0	0	8	1,1	2	1	0	3	1,22	1	0	0	1	1,2	0	1	3	4	1,21	0	0	1	1
1,41	2	0	0	2	1,26	1	1	0	2	2,2	0	2	3	5	1,25	0	3	0	3	3	0	0	3	3
1,42	2	0	0	2	1,46	2	0	0	2	2,4	0	0	3	3	1,8	0	3	0	3					
1,45	3	0	0	3	1,7	0	1	0	1	3,1	0	1	2	3										
4,11	2	0	0	2	7,4	7	0	0	7															
4,2	3	0	0	3																				
Sum	20	0	0	20	Sum	12	3	0	15	Sum	1	3	8	12	Sum	0	7	3	10	Sum	0	0	4	4
4,1(?)	3	0	0	3																2(?)	0	0	3	3
6(?)	3	0	0	3																Sum(?)	0	0	7	7
Sum?	26	0	0	26																				

TABLE XVII. Heredity of pattern-shape.

It ought also to be remembered that the character of the median shape of the finger-patterns has not yet been sufficiently studied. We do not yet know whether this median group represents heterozygotes, or whether with its arbitrarily fixed border-lines it represents only the overlapping caused by a fluctuating variation within the extreme groups.

Until these questions have been decided with a larger material no definite result can be reached as to the type of heredity of the circular-elliptical shape of finger-patterns.

With regard to the numerical occurrence of the circular and elliptical pattern-shape it seems evident that the former is by far the most frequent, even if the elliptical shape occurs frequently enough among human families for omitting the rather discriminating name of "Simian type," previously applied upon such patterns. My family material gives, however, no true picture of the numerical relations between circular and elliptical pattern-shape, the latter being probably too amply represented because of the high interest attached to the study of this type.

(β) *Twisting tendency. Double loops and their derivatives.*

As demonstrated already in Figs. 14–17, both circular and elliptic patterns may be complicated through a more or less pronounced tendency to twisting, the papillary ridges forming not concentric figures or simple spirals, but double spirals or double loops more or less intimately twisted round each other. We have seen also that from the various types of double loops there exist series of transitions partly into simple loops and partly directly into arches.

The twisting tendency has in our analysis of papillary patterns been proved to appear independently of the circular-elliptical shape of patterns, as well as of their quantitative value. Before turning to the question of the heredity of this new character it will be necessary to take a survey of its general occurrence.

As shown in Table XVIII, the appearance of twisted patterns is very much more frequent upon digit I (48 per cent.) than on any of the other fingers, nearly so, indeed, as on all the others taken together. Digit V, on the other side, has a very low percentage (6·4 per cent.) of twisted patterns, while they are more equally distributed upon the three median fingers (12·8–17 per cent.). A strange feature in the distribution of twisted pattern is seen in their greater frequency upon left hands (56·7 per cent.) than upon right ones (43·3 per cent.), a distribution which is valid, not only for the hands taken as a whole, but also for each of the four

first fingers; an opposite relation upon digit V of right (7) and left (4) hands may, indeed, not be considered contradictory to this rule, the figures here being too small for giving a reliable result.

Dig.		I		II		III		IV		V			
Hand		r	l	r	l	r	l	r	l	r	l	Sum total	%
Twinned	uln.	25	39	4	6	7	12	10	18	7	4	132	77.2
	sym.	5	1	1	3	1	1	0	0	0	0	12	7
	rad.	6	6	8	5	0	1	0	1	0	0	27	15,8
Hand	r	36		13		8		10		7		74 43.3 %	171
	l		46		14		14		19		4	97 56.7 %	
Sum total		82 (48%)		27 (15,8%)		22 (12,8%)		29 (17%)		11 (6,4%)			

TABLE XVIII. Tendency to twisting. Distribution in percentage of all twisted patterns.

This very special distribution of twisted patterns upon the various fingers is a strong indication of their dependence upon the shape of the apical pad of the finger. Their great preponderance upon digit I would indicate some causal connection with the broad balls of this finger, and —if this be the case—their frequent occurrence, especially upon left fingers, would further indicate that the finger-balls of left hands are, generally speaking, more flattened than those of the right.

It may be of interest for the whole characteristics of the fingers to cast a glance also at the numerical relations between the regular, untwisted whorls, and the twisted patterns (double loops and their derivatives) which, in the general statistics, are considered as whorls because of their having two triradii.

A survey of such relations is given in Table XIX, showing the whorls of all fingers divided into two groups according to their being twisted or not. Here, again, we find a very conspicuous difference between digit I and all the others. While upon digit I of right and left hands 53·9 per cent. and 79·6 per cent. respectively of all whorls prove to be twisted, we find a much lower percentage (10–25) of twisted whorls upon all other fingers.

Of special interest is a comparison between digit I and digit IV, these two fingers being, in all human races investigated (see p. 23 and Tables V–IX), very similar with regard to the statistics of papillary patterns, so long as statistics are based only upon the three main types of patterns—whorls, loops and arches. As a special characteristic of both fingers has been noted their extraordinarily high percentage of whorls. We now see that these whorls of digit I and digit IV respectively are, to a great extent, of a different character, those of digit IV representing mostly (90 per cent. and 80·6 per cent. upon right and left hands) regular untwisted whorls, while upon digit I of both hands the great mass of whorls are in reality double loops, only a relatively small number (46·1 per cent. and 20·4 per cent.) being ordinary whorls.

Dig.	I				II				III				IV				V			
Hand	r		l		r		l		r		l		r		l		r		l	
Number	abs.	%	abs.	%	abs.	%	abs.	%	abs.	%	abs.	%	abs.	%	abs.	%	abs.	%	abs.	%
Whorls T	34	53,9	47	79,6	14	17,5	12	15,8	5	14,3	11	25	10	10	15	19,4	5	19,2	2	11,1
Whorls R	29	46,1	12	20,4	66	82,5	64	84,2	30	85,7	33	75	89	90	62	80,6	21	80,8	16	88,9
Sum	63	100	59	100	80	100	76	100	35	100	44	100	99	100	77	100	26	100	18	100

TABLE XIX. Whorls, regular or twisted. Statistics.

This fact supports what was said above about a causal connection between the special broad shape of digit I and the development of double loops upon its distal phalanx. Such a connection would, however, in no way interfere with the tendency to twisting being at the same time an hereditary character. As already mentioned, we should, in our analysis of the papillary patterns, always remember that any particular feature of these patterns ought, perhaps, to be considered as a visible expression of some change within the finger-ball itself, a change which, of course, may be either hereditary or not hereditary. If, on the other hand, the twisting tendency should prove to be due to an hereditary factor directly influencing the papillary pattern, then the causal connection between the latter and the finger-ball would be that of a genotype, the phenotypical expression of which depends upon certain conditions of life promoting or preventing its development. In both cases a frequent appearance of twisted patterns in certain families, together with its non-appearance in others, would indicate hereditary influence. The dependence between balls and patterns will, in both cases, cause the unequal development of the twisting upon various fingers, or even prevent

its appearance on such fingers where the conditions of the pads are not favourable for its development.

A survey of the minutely analysed material of the finger-prints from 174 individuals proves one or more twisted patterns to exist in 76 individuals (43·6 per cent.). Among these, again, 31 persons (18 per cent. of all) carry twisted patterns upon their digit I only, while in the rest such patterns occur also on digits II–V, in the distribution shown in Table XVIII.

In the pedigrees we find examples of families which give a strong impression of an hereditary nature of the twisting tendency (T). Thus in Fams. 1, 2 and 5 the twisted patterns are very common, while in Fams. 3, 4 and 6 they scarcely exist. The numerical relations of the occurrence of twisted and regular patterns in parents and children are shown in Table XX, in which all families of our pedigrees are grouped according to the existence or absence of twisting in the patterns of the parents.

Parents: T×T				Parents: T×R																Parents: R×R			
Fam.	Children T	Children R	Children Sum	Fam.	Children T	Children R	Children Sum	Fam.	Children T	Children R	Children Sum	Fam.	Children T	Children R	Children Sum	Fam.	Children T	Children R	Children Sum
1,1	2	1	3	1,2	2	2	4	1,25	3	0	3	7,4	1	6	7	1,21	0	1	1
1,22	1	0	1	1,26	1	1	2	1,4	7	1	8					1,41	0	2	2
1,42	2	0	2	1,45	1	2	3									3	0	3	3
1,8	3	0	3	1,46	1	1	2									4,2	0	3	3
2,4	3	0	3	1,7	0	1	1												
				2,2	2	3	5												
				3,1	1	2	3												
				4,11	1	1	2												
	11	1	12		9	13	22		10	1	11		1	6	7		0	9	9
									20	20	40								

TABLE XX. Tendency to twist; heredity.

In all cases in which both parents have only untwisted, regular patterns ($R \times R$), four families with together nine children, none of the children have shown any tendency to twisting. In the corresponding group at the other end of the table, in which both parents have twisted patterns ($T \times T$), one child (Fam. 1, 1) was found with only regular patterns. All other (11) children, however, of such matings show the

development of twisting. The families, 11 in number, in which one parent has twisted and the other regular patterns ($T \times R$), have in all 40 children, 20 with twisted and 20 with regular patterns.

All this might indicate a simple dominance of twisting (T) over regular (R), the T-parents being to a great extent heterozygotes; such might, for example, be the case with all the families of the second column of our table with a sum total of 22 children, nine of which have twisted while 13 have only regular patterns. In the two families of the third column in which, among 11 children, ten have twisted patterns, one of the parents might perhaps be a homozygous dominant, all children showing, therefore, phenotypically the dominant character, which has, however, for some reason been suppressed in one child of Fam. 1, 4. But as a contrast we find in column 4 a very different case, in which no less than six children have regular patterns, while only one has shown a faint tendency of twisting.

The facts here presented, sufficient to prove the hereditary nature of the twisting tendency of papillary patterns, therefore, give as yet no satisfactory demonstration of the type of heredity. If this heredity should in future prove to be that of a simple Mendelian dominance of T over R, some modifying factor would be necessary to account for cases like those of the families 1, 4 and 7, 4. The numbers of individuals as yet at our disposal are, however, too small to justify definite conclusions.

The heredity of the pattern-design, now proved through a consideration of the characteristics of parents and children in different families, may perhaps be as clearly demonstrated through a comparison of the whole pictures represented by the patterns of different members, or even generations, of one and the same family.

As mentioned above (p. 64) it is very difficult to find patterns forming harmonious series of transitions between whorls and loops or arches, or between double loops and arches, if the pictures are not taken from nearly related persons. Already this fact is an indication of the existence within each family of a certain genotype which determines the main lines of the pattern-shape. The degree of development of such a genotype will, as already shown, in each pattern, depend first upon the *quantitative value of the individual* to which it belongs and, secondly, also upon the characteristics of each special finger.

An illustration of this is given in Fig. 31 showing finger-patterns from three generations of one and the same family (Fam. 1, 2, Pl. III). In the first line of this figure we find the patterns of digit IV of left and right

hands of a man 60 years old (1, 2[1]). In accordance with what has been said above with regard to the analysis of patterns, we recognise in these pictures patterns with an elliptic shape (E) and with a marked tendency to twisting (T). The quantitative value of the right-hand pattern is 9·5, its radial and ulnar side presenting respectively the classes 10 and 9; the left-hand pattern has a value of 8·5, both sides belonging to classes 10 and 7 respectively.

With regard to the course of the papillary ridges we see upon the right digit IV a double loop, the inner ends of which, as a consequence of the elliptic shape of the pattern, are approximately parallel to the longitudinal axis of the finger, one loop descending towards the proximal, the other ascending towards the distal end of the phalanx. This double loop is, however, not fully developed, its ascending branch being, as it were, narrowed at its base, so that only its peripheral ridges are continued, and can be traced as taking part in the formation of the outer, elliptic part of the pattern, the central ridges of this ascending loop not being continued. On the left digit IV this same process is further developed, the ascending inner end of one loop being quite cut off from its more peripheral continuation, and isolated as a nucleus in the centre of the pattern ("Amygdalus" Purkinje; "Amande" Alix, etc.). In this pattern the longitudinal ridges of the right digit IV have taken a more oblique course so that the proximal end of the pattern turns towards the ulnar side of the finger.

The two next lines of the same Fig. 31 show five patterns from two sons of the man first studied, 1, 23 and 1, 25. In all these pictures we find the same elliptical shape (E) characteristic of the patterns of the father. This shape is seen even in the much reduced pattern of digit II *l.* of Nr. 1, 25, in which a loop containing only a few ridges has still a very considerable height. In this latter pattern no twisting can, of course, be seen; but in all the others we find very conspicuous traces of a twisting tendency (T) of the ridges. The quantitative value of these twisted patterns varies from 9·5–6; corresponding to the sinking value we find also a series of pictures illustrating the reduction of the double loop, already pointed out for the father, from a fully-developed double loop with longitudinally running ridges in the descending and ascending inner ends (Nr. 1, 25, digit I *l.*) to a more or less complete isolation and reduction of the ascending loop (Nr. 1, 25, digit III *l.*; Nr. 1, 23, digit IV *l.* and digit IV *r.*).

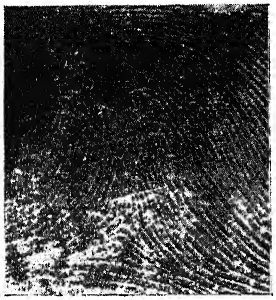
In the fourth line, finally, some pictures are given from the third generation of this same family, viz. one picture from each of three children

Nr. 1,2^1. Dig. IV *l.* *E–T* 8·5.

Nr. 1,2^1. Dig. IV *r.* *E–T* 9·5.

Nr. 1,23. Dig. IV *l.* *E–T* 6·5.

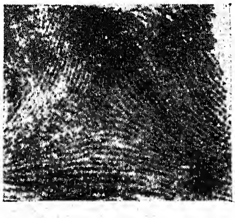
Nr. 1,23. Dig. IV *r.* *E–T* 6.



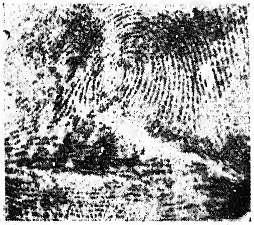
Nr. 1,25. Dig. II *l.* *E* 2.

Nr. 1,25. Dig. III *l.* *E–T* 8·5.

Nr. 1,25. Dig. I *l.* *E–T* 9·5.



Nr. 1,252. Dig. II *l.* *E* 1·5.



Nr. 1,253. Dig. IV *l.* *E–T* 6·5.

Nr. 1,251. Dig. I *l.* *E–T* 5·5.

Fig. 31. Finger-patterns from six individuals belonging to three generations of one and the same family, all showing the same design (*E–T*), characteristic of many members of this family.

of Nr. 1,25. The first picture in the fourth line (Nr. 1,252, digit II *l.*) shows in connection with the one placed above it the similarity between the patterns of corresponding fingers of father and daughter, both having the relatively rarely occurring long and narrow loops which indicate the elliptic shape of the patterns, and which through further reduction would give the so-called "tented arch." The two other pictures of the fourth line, again, fully correspond to those described above from grandfather, father and uncle of these children, showing the elliptic shape, and also a more or less reduced remnant of an ascending loop, that is, an indication of the twisting tendency.

It may be of interest here to note the close correspondence between the two pairs of pictures forming the right side of Fig. 31, the two upper ones showing one and the same finger (digit IV *r.*) in father and son, the two lower ones likewise showing corresponding fingers (digit I *l.*) in father and son of the following generation. The similarity between the patterns forming the two links of each pair is, indeed, not very great, but the close correspondence between both pairs as a whole is in itself a strong indication of a genetic relation between both these patterns.

The whole series of patterns here considered seems, indeed, to be nothing but a series of different stages of development of *one and the same genotypical design* containing the factors necessary for the elliptic shape (E) and for the twisting tendency (T). The difference between the patterns depends, partly at least, upon the third group of factors necessary for the development of papillary patterns, those of their quantitative value.

I may also mention that the pictures shown in Fig. 31 are not the only ones from this same family which correspond in the manner above described. Many others were found, in other individuals and upon other fingers of the individuals already represented. Similar pictures might further be found also in any family in which the papillary patterns have a twisting tendency combined with an elliptic shape.

Corresponding series of pictures might also easily be demonstrated from other families with e.g. circular patterns (C), which again may be either twisted (T) or regular (R). It will, however, be sufficient to draw the attention of the reader once again to the pictures demonstrated in Fig. 14 (p. 40) from various fingers of a pair of twins (1,12 and 1,13) with circular, twisted patterns, as well as to Fig. 16 (p. 42) from two generations of another family (Fam. 1,4) also with circular, twisted patterns. The difference between the two latter groups of patterns and that of Fig. 31 (also represented in Fig. 17) is at once conspicuous.

(γ) *Minor characteristics of patterns.*

In the analysis of papillary patterns, besides the characters mentioned regarding the whole shape of the pattern, one meets with minor details[1] in the arrangement of the papillary ridges. Some of these are certainly heritable, being found in groups of nearly related individuals. I shall here only, by demonstrating a few examples, draw the attention to such characteristics, being confident that our knowledge of them will rapidly increase through a further analysis of any new material.

The pictures of Fig. 32 are taken from a woman (Nr. 5, 2) and her nephew (Nr. 5, 42).

Nr. 5,2. Dig. III *l.*

Nr. 5,2. Dig. II *l.*

Nr. 5,42. Dig. III *l.*

Nr. 5,42. Dig. III *r.*

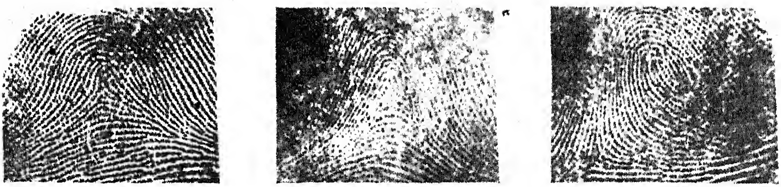
Fig. 32. Finger-patterns from a woman (5, 2) and her nephew (5, 42), all showing the same minor characteristics.

In the pattern of digit III *l.* of this woman, we find a special form of double loop (so-called "lateral pocket loop") in which the two loops are not, as usual, spirally twisted round each other, but have their axes running out parallel towards one side of the pattern, as in a common

[1] Not to be confounded with the *minutiae* of each single ridge, so important to the identification of individuals.

single loop. The doubleness of the loops is in this case shown at the top only, where the upper loop, longer than the other, bends down so as to form a sort of mantle round the lower one. Both digits III of her nephew have patterns which would be classified as loops, but with irregularities in the course of their ridges very obviously recalling the characteristic pattern of the aunt. The slight irregularity of digit II *l.* of the aunt, one single ridge turning backwards to form a tiny loop over the top of another, a peculiarity which, if isolated, easily might escape observation, should probably also be looked upon as a trace of this same characteristic.

Another example of such minor characteristics is shown in Fig. 33, all the patterns of this figure being, however, found in one individual



Nr. 1, 252. Dig. II *r*. Nr. 1, 252. Dig. III *l*. Nr. 1, 252. Dig. IV *r*.

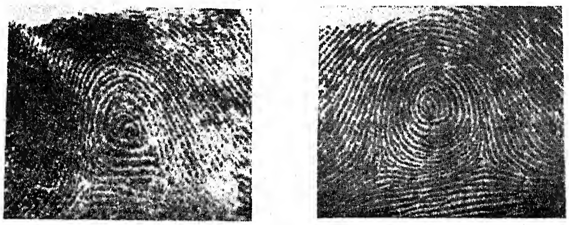
Fig. 33. Three patterns from the fingers of one individual (1, 252), showing minor characteristics.

only (Nr. 1, 252) and no heredity being as yet perceived. The first picture (digit II *r.*) shows, as in the above example, a special configuration of double loops, both being of very low value. The central part of the pattern is formed by a small loop consisting of three ridges in all, and opening towards the ulnar side of the finger. Another loop, opening towards the radial side, here again forms a sort of mantle round the top of the former; this second loop is, however, peculiarly pointed at its top, where, of three converging lines, two unite at an acute angle. The next picture (digit III *l.*) shows another configuration built upon the same design. Instead of the lower loop we here find in the centre of the pattern a few highly arched lines, running from side to side of the pattern, but giving somewhat the same outline as the central loop of the pattern of digit II *r*. Above this arch we find, again, the mantle loop, opening here towards the ulnar side of the finger, but having at the other side the same peculiarly pointed top formed by converging ridges meeting at an acute angle. The third picture finally, digit IV *r.* of the same individual, would alone scarcely have called for our attention; it would in the general classification be considered a common loop. But even here we find some faint indications of the same plan, which is more conspicuously presented

in the two other patterns. In the loop, now before us, we find again a few central ridges running parallel out towards the ulnar side of the finger; but these lines are at their top surrounded by a group of other ridges (representing the mantle loop?), running at one end parallel out towards the ulnar side, while at the other end the ridges converge so as to form a mantle round the central loop.

An attentive consideration of the three pictures here described will show the direction of the two loops to vary from one pattern to the other. Such inversion, however, is not surprising when we consider first, that upon digit II we very often find a change of direction of any pattern-type, the radial direction being here very common, and, secondly, that very low-valued patterns may, upon any finger, vary considerably with regard to direction. As mentioned above, the hereditary character of the peculiarity described has in this case not been proved. The family of the mother has, however, not yet been investigated, and from my experience in other families I should think it very probable that similar peculiarities might be found there.

Finally, an example may be given of minor characteristics of a very different type. Fig. 34 gives patterns from mother and son, both patterns



Nr. 1, 25. Dig. III *l*. Nr. 1, 251. Dig. II *r*.

Fig. 34. Finger-patterns from mother (1, 25) and son (1, 251), representing small, symmetrical whorls.

representing a relatively rare type, that namely of low-valued, but nevertheless symmetrical whorls. Generally the symmetry of a whorl-design is lost as soon as the pattern is more or less checked in its development, one delta only reaching its designed distance from the centre. The occurrence of such rare pictures in mother and son is a fact which may perhaps indicate its hereditary nature.

What has been said above about such minor characteristics of papillary patterns is, as yet, insufficient to justify definite conclusions. It ought to be considered only as an introduction to a chapter on the heredity of papillary patterns, which for its accomplishment needs future investiga-

tion of abundant and thoroughly analysed material. As mentioned already by Cevidalli (1911) such investigation may prove important as a means of indicating relationship between individuals.

(c) *Direction of Finger-Patterns.*

The indications radial and ulnar have in the literature of papillary patterns been used for loops only. Statistical results have (see Table IX A) for all human races investigated proved a high proportion of radial loops to be one of the specific characteristics of digit II, and we have (p. 30) suggested a causal connection to exist between this occurrence of radial loops and the importance of the radial side of the finger-ball of this special finger as working opposed to the thumb.

The indications radial and ulnar ought, however, by the same right to be applied also to all patterns transitional between symmetrical whorls and loops, the direction of the reduced pattern being always distinctly characterised through the number of ridges upon each side between the triradius and the centre of the pattern (see p. 48). Even with regard to the arches, a number of patterns exist in which one triradius is still present, indicating a certain direction of these patterns also. For any discussion, therefore, of the question of heredity of pattern-direction, not only the loops but also the whorls and arches should be taken into consideration.

A statistical survey of the pattern-direction is given in Table XXI including 1740 fingers. A relatively small number of whorls and arches (9·89 per cent. of all patterns) are absolutely symmetrical. Besides these we find of ulnar patterns 1372, or 78·85 per cent., while only 196 patterns (11·26 per cent.) are radial. The distribution of radial patterns upon each of the ten fingers is very unequal, the great majority (76 per cent.) being, as was the case also with radial loops, found upon digit II, somewhat more upon right hands than upon lefts. 13·3 per cent. of radial patterns are found upon digit III, 8·2 per cent. on digit I, 2·5 per cent. on digit IV, and on digit V none.

Symmetrical patterns are found also to have their maximum frequency (33 per cent.) upon digit II, and upon digit V their minimum (3·5 per cent.). But the difference between these two extremes is not nearly so wide as was the case with the radial patterns.

The ulnar patterns, including 78·85 per cent. of all fingers, consequently find their maximum at digit V (24·9 per cent.), while digit II presents their minimum (10·4 per cent.).

A discussion of *heredity in pattern-direction* must, of course, be based

upon this knowledge of their statistical occurrence upon different fingers. Thus, digit II, of which the great frequency of radial patterns seems to be characteristic, ought not to be made the basis for hereditary investigation of this point. The question to be solved is, rather, that of the

		Direction of Finger-patterns.									
Finger	Hand	Radial			Ulnar			Symm.			Number of fingers
		Abs		% of type	Abs.		% of type	Abs.		% of type	
I	r	7	16	8,2	143	292	21,3	24	40	23,3	348
	l	9			149			16			
II	r	80	149	76,0	67	142	10,4	27	57	33,0	348
	l	69			75			30			
III	r	8	26	13,3	144	282	20,5	22	40	23,3	348
	l	18			138			18			
IV	r	4	5	2,5	155	314	22,9	15	29	16,9	348
	l	1			159			14			
V	r	0	0	0	171	342	24,9	3	6	3,5	348
	l	0			171			3			
Sum total			196	100,0		1372	100,0		172	100,0	1740
% of fingers			11,26 %			78,85 %			9 89 %		

TABLE XXI. Direction of finger-patterns. Statistics.

rarely occurring radial patterns, upon other fingers, e.g. digits I or III, whether or not their occurrence is due to heredity.

Radial patterns upon digit III occur, in the whole material of 348 hands, 26 times in all, but in the pedigrees only in 12 individuals, four of whom belong to one family (mother, 7,4 and three children, 7,41–7,42–7,45), five to another (three sisters, 5,2–5,3–5,4, and two children, 5,21–5,22, of one of them). In two other families (Fams. 3 and 4) radial patterns upon digit III of one (3,11) or two (4,12, 4,112) individuals are found besides symmetrical patterns on the same finger of others (0, 3,1, 3,11 and 4,1, 4,111) belonging to the same branch of the family. In other families, as e.g. the great Fam. 1, no case of radial pattern upon digit III occurs.

Radial patterns upon digit III may in rare cases (5,22) be accompanied by the same direction of pattern also upon digit IV.

This concentration of examples of a relatively rare pattern-direction within certain family branches seems to indicate the hereditary nature of this character.

The observations are, however, as yet too scanty to allow definite conclusions to be drawn with regard to heredity.

The occurrence of radial patterns upon digit I is still more rare than upon digit III, 16 cases only having been observed in the 348 hands (4·6 per cent. of all digits I). The two fingers mentioned seem to be independent of each other with regard to their pattern-direction, in so far as in my material the radial direction of their patterns occurs in different family branches. Thus in Fam. 1, in which no case occurs of radial patterns upon digit III, no less than seven individuals exist with a radial direction of their patterns upon digit I.

Here, however, no case indicates a simple dominant heredity from one generation to the next. The occurrence of radial patterns upon digit I is, indeed, so intimately connected with the existence of more or less developed double loops, that I can scarcely look upon it as any independently hereditary character.

CHAPTER 7.

Finger-Patterns of Identical Twins.

Discussion on heredity of patterns has, especially by Wilder (1904 *b*, 1908, 1916, 1919) and Poll (1914) been based upon an investigation of such structures in presumably identical (duplicate) twins. In my material such twins also occur, and it may be of interest, by an investigation of their patterns, to control the results reached with regard to the various hereditary characters. If such characteristics have been seen in one of a pair of identical twins, they ought also to be found similarly developed in the other, while conversely special peculiarities found in the patterns of both twins ought, for this reason, very probably to be considered as hereditary.

The authors agree in the result that the patterns of twins are never fully identical. Thus Wilder, studying the whole configuration of the palms, declares (1919, p. 411): "The correspondence in the friction-skin configuration is confined to the general plan of the surface as a whole and does not extend in the least to the finer details, the 'minutiae' of Galton." And Poll has during his investigation of finger-prints of identical twins reached a similar result, saying (1914, p. 95): "Immer kommen lediglich Ähnlichkeiten in Frage, also teilweise Gleichheiten, begleitet und untermischt von Unterschiedlichkeiten."

Wilder (1904 *b*), after having investigated nine sets of true duplicates, mentions as features of special interest (p. 440): "(1) the tendency to a symmetry between the two sides, which appears to be far greater than among other individuals, and (2) the mysterious reversal of index patterns of one hand or the other." The view first mentioned was maintained by Wilder not only for the finger-patterns but, more especially perhaps, for the markings of the whole palms which have been thoroughly investigated by him.

With regard to the reversal of the index-pattern Wilder refers to the theory of transposition of viscera in twins[1], and especially Bateson's statement (1894) that the transposition need not necessarily be a complete one. He adds, however (p. 442): "But why the transposition should affect one finger alone, or why that finger should always be the index, these are at present questions beyond solution." This same question is touched by Wilder also in later papers. Thus in his very valuable paper of 1916 he maintains (p. 211) for twins of the true duplicate type as a condition "not absolutely constant, but frequently noted, a reversal of the pattern of the index fingers in the two individuals, affecting either the two right hands or the two left hands, or occasionally both sets."

In view of the statistical evidence given in this paper the occurrence of reversal of the index pattern will not surprise, such reversal being acknowledged as a common characteristic of all human races investigated. According to my experience it does not occur more frequently in twins than in other persons; nor does it occur so schematically distributed upon the hands of twins as maintained by Wilder. Here, as elsewhere, a reversal of the pattern upon the index may often be found upon one hand only, without being found in the corresponding finger of the other twin (see, e.g., Fig. 36, digit II *l.*).

The question of symmetry in duplicate twins is elucidated also by the work of Newman and Patterson on the development of the Armadillo quadruplets, and especially that of Newman (1915–16) upon heredity of scute anomalies. Duplicate twins as well as quadruplets, being originally parts of one developing unity, must originally also have formed parts of one common system of symmetry. Applied to the papillary patterns this implies that a pair of identical twins ought to represent, one the fingers of an original right hand, the other those of the left. But after their separation each individual will, as shown by Newman for Armadillos, develop a new system of symmetry between the antimeric

[1] This question has later been treated, for artificially produced twins of *Triton*, by Spemann and Falkenberg (1919).

halves of their body. The original symmetry between twins will, therefore, in part only, be retained, and in part obliterated by the new antimeric symmetry. "It appears to be a good general rule," says Newman (1916, p. 203), "that the earlier the separation the more complete is the reorganization of symmetry relations in the separated individuals and the less the residuum of the original common symmetry."

This question about the symmetry of identical twins is one of great general interest. Some new facts regarding it will be given below.

Poll (1914) proposes as a basis of comparison of finger-patterns a sort of scale marking three different grades of similarity. He says (p. 96): "Der höchste, dritte, Grad der Ähnlichkeit kennzeichnet sich durch gleichzeitiges Zusammentreffen von Gleichheit, (1) des Mustertypus oder der Mustervarietät selbst, (2) der Stilart der Musterzeichnung, (3) der Zahlenklasse der zur Bildung des Musters verwandten Papillarlinien.

"Ähnlichkeit zweiten Grades wird angenommen wenn Muster und Stil übereinstimmen, die Grössenklassen der Leistenzahlen aber verschieden sind.

"Ähnlichkeit ersten oder niedersten Grades findet statt, wenn sich nur die Muster als solche in Typus und Unterart gleichen."

From the point of view maintained in the preceding chapters the "type" or even "variety" of the pattern should, in a discussion of natural relationship between patterns, hardly be made the basis of comparison. The same genotypical plan may, according to special characteristics of each finger-ball, be developed, to a whorl upon digit IV, while upon digit V it would appear as an ulnar loop, and on digit I perhaps as a double loop.

The two other characters mentioned by Poll, "der Stilart" and "die Zahlenklasse," which probably correspond to the *design* and the *quantitative value* of this paper, will, however, if systematically applied to all patterns, give a fully sufficient basis of comparison. Upon this point my investigation of the patterns of twins has fully supported the views maintained in the previous chapters.

The number of twins contained in my material amounts to 31 pairs of unisexual twins, mostly school children. Out of these twins, ten pairs (Group IV of Fig. 35) should, without doubt, be considered as being only fraternal, because of their very slight facial similarity. Thirteen other pairs (Groups II and III) with a more or less conspicuous similarity have been grouped as being questionable, the resemblance being, however, in seven of them (Group II) so great that these should very probably be considered as identical twins. This is the case also with the remaining eight pairs of my twin material (Group I), in which the facial similarity

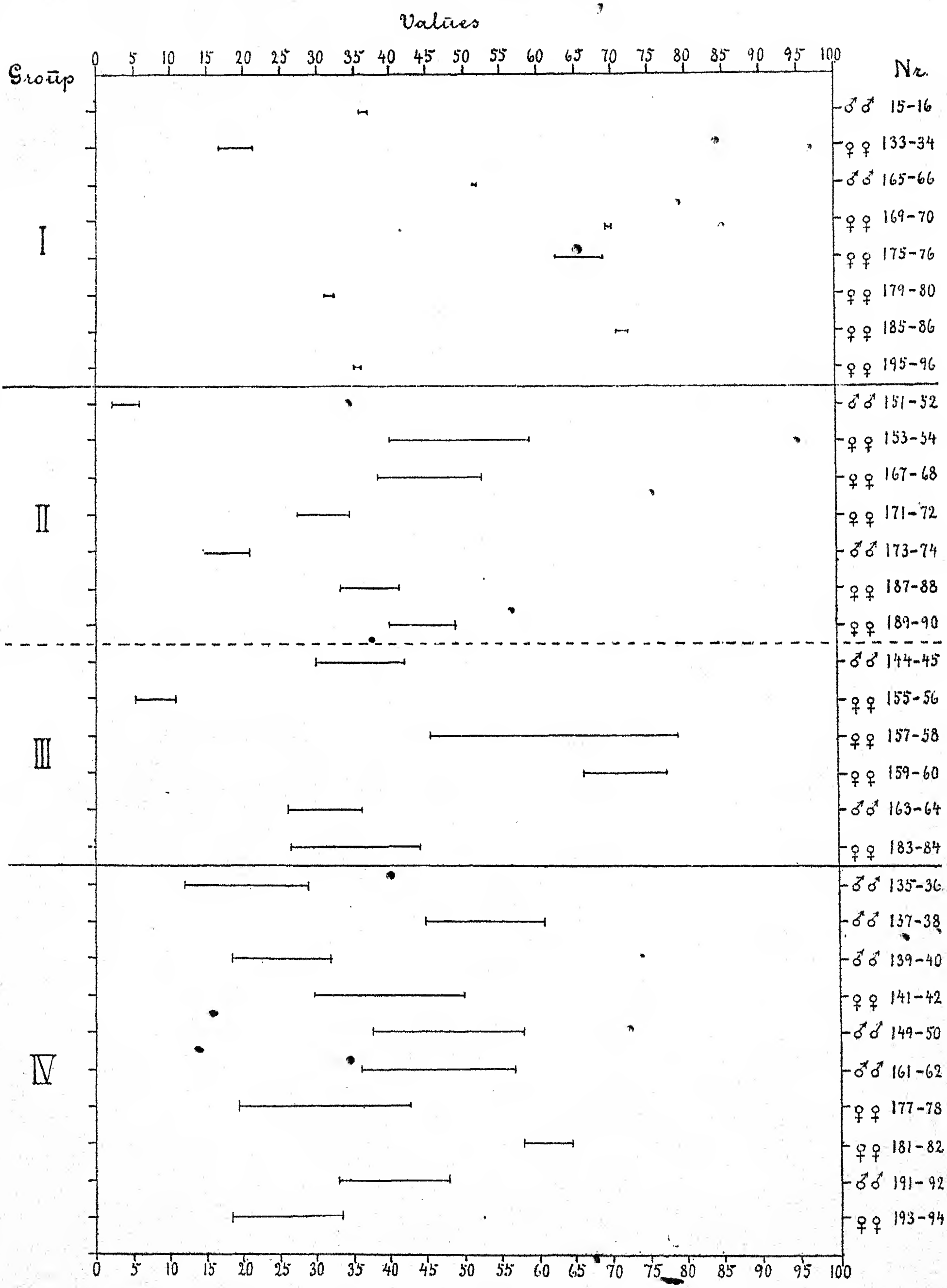


Fig. 35. Quantitative values of 31 unisexual twin pairs, combined to Groups I–IV, according to the facial similarity of the twins. Groups I and II have, in the calculations of correlation, been considered as identical twins, Groups III and IV as fraternal.

is very striking. Thus, although no definite information has been obtained with regard to the mono- or dizygotic origin of the twins, I shall probably not be wrong in considering the 15 last-named pairs (Groups I and II of Fig. 35) as representing identical twins, while the other 16 pairs (Groups III and IV) are looked upon as fraternal twins.

The quantitative values of all the twins, arranged into groups in the way just mentioned, are shown in Fig. 35, where the values of each twin pair has been marked upon a horizontal line in the same manner as that used for the families of Fig. 29 *a–b*.

Fig. 35 proves a close correspondence to exist between the general resemblance (identity?) of the two members of a twin pair and the resemblance also of their quantitative pattern-values. A comparison of the twin pairs of Group I with those of Group IV gives a clear demonstration of this fact, while the more questionable groups, II and III, with regard to the quantitative values, illustrate transitions between these two extremes. In Group I several twin pairs prove, indeed, to have quantitative pattern-values very nearly identical. In view of the fact that the two hands of one and the same individual very seldom are exactly alike, and that they often may show considerable difference with regard to their quantitative values, the correspondence just mentioned between the two members of one twin pair provides a remarkable demonstration of symmetry between identical twins.

According to the results of Wilder an unusual degree of symmetry was to be expected not only between the patterns of the two members of a twin pair, but also between the two sides of each twin individual. I have, in my material, seen many examples of such symmetry between right and left hands of twins; indeed, I believed at first that my own results upon the finger-patterns supported the view maintained by Wilder for the markings of the whole palms. A more thorough consideration of this question has proved the symmetry of pattern-values between right and left hands of twins to be not essentially different from that of single individuals.

The symmetrical relations of twins with regard to their patterns are illustrated by the figures given in Table XXII, which again have been utilised for a calculation of the coefficients of correlation given in Table XXIII. A comparison, first, between arbitrarily paired unrelated individuals (column I of Table XXII) will, of course, give a very low coefficient of correlation, in our case $r = -0{\cdot}27 \pm 0{\cdot}128$. The correlation of pattern-values between brothers and sisters (column II) is, however, considerably higher, $r = 0{\cdot}595 \pm 0{\cdot}118$, and for our material of fraternal

I Unrelated individuals			II Brothers and sisters			III Fraternal twins		IV Identical (?) twins				V Single individuals		
										Hands			Hands	
Nr.	A	B	Nr.	A	B	Nr.	A,B	Nr	A,B	right	left	Nr.	right	left
1-7	50,73	52,95	8-9	59,14	69,48	135	11,5	15	35,48	21,57	13,91	1	25,63	25,10
10-11	18,30	53,42	20-21	74,38	78,66	136	27,0	16	36,76	17,97	18,79	7	25,77	27,18
12-17	43,78	92,96	33-34	57,05	62,45	137	61,5	133	21,37	11,61	9,76	8	29,30	29,84
18-19	32,37	35,46	38-39	65,90	48,63	138	44,0	134	16,86	9 19	7,67	9	31,38	38,10
22-23	69,52	48,30	39-40	48,63	53,75	139	32,0	151	2,54	0	2,54	10	11 95	6,35
24-25	60,81	34,75	41-44	63,70	27,18	140	18,5	152	6,06	2,46	3,60	11	25,71	27,71
27-28	60,28	37,36	42-43	50,75	72,49	141	29,0	153	59,11	26,76	32,35	12	20,72	23,06
29-30	23,64	34,82	45-46	84,54	52,29	142	48,5	154	40,22	22,01	18,21	17	46,43	46,53
30-31	34,82	92,68	47-48	33,70	39,95	144	30,5	165	59,19	26,09	25,20	18	16,40	15,97
35-37	60,83	38,02	51-52	49,86	31,11	145	42,0	166	51,83	26,18	25,65	19	18,46	17,0
40-41	53,75	63,70	52-53	31,11	46,38	149	37,0	167	52,78	26,03	26,75	20	40,63	33,75
44-45	27,18	84,54	60-61	45,08	67,09	150	57,5	168	38,83	18,08	20,75	21	42,48	36,18
46-47	52,29	33,70	61-62	67,09	63,98	155	11,0	169	69,17	34,99	34,18	22	38,32	31,20
48-49	39,95	30,90	59-69	74,04	64,60	156	5,0	170	70,33	34,31	36,02	23	23,38	24,92
50-58	40,52	42,18	8-71	59,14	67,39	157	44,5	171	27,52	16,30	11,22	24	30,40	30,41
58-59	42,18	74,04	73-74	21,63	5,75	158	78,5	172	34,96	16,34	18,62	25	17,23	17,52
62-63	63,98	24,73	74-65	5,75	10,20	159	76,5	173	21,14	9,83	11,31	27	27,73	32,55
65-69	10,20	64,60	76-7	44,58	52,95	160	67,0	174	14,93	7,91	7,02	28	17,91	19,45
70-71	65,56	67,39	79-80	49,81	44,32	161	36,0	175	62,60	32,40	30,20	29	9,26	14,38
74-75	5,75	57,71	81-82	34,82	55,15	162	57,0	176	69,20	39,29	29,91	30	15,86	18,96
77-79	44,29	49,81	82-83	55,15	57,96	163	37,0	179	32,46	14,26	18,20	31	47,80	44,88
80-81	44,32	34,82	84-24	30,21	60,81	164	25,0	180	31,58	14,71	16,87	32	34,35	40,06
83-84	57,96	30,21	85-143	69,92	61,63	177	42,5	185	70,40	36,98	35,42	33	29,99	23,06
109-110	76,89	13,98	87-88	69,06	59,48	178	19,5	186	70,94	39,72	31,22	34	32,80	29,65
113-115	34,40	50,64	90-91	41,65	42,57	181	64,5	187	41,29	21,51	19,78	35	31,75	29,08
115-116	50,64	26,30	91-92	42,57	43,01	182	58,0	188	33,64	15,89	17,75	37	16,18	21,84
119-121	57,20	80,05	94-95	57,16	48,13	183	44,5	189	40,05	18,06	21,99	38	27,50	38,40
122-123	52,41	68,34	95-96	48,13	55,83	184	27,5	190	49,18	24,88	24,30	39	22,23	26,40
130-131	5,82	36,67	99-100	32,36	19,19	191	48,0	195	35,37	19,20	16,17	40	28,76	24,99
132-133	60,79	21,37	102-105	34,90	47,24	192	33,0	196	36,29	18,38	17,91	44	10,64	16,54
						193	18,5							
						194	33,5							

TABLE XXII. Quantitative values of identical (?) twin-pairs (column IV) as compared with those of fraternal twins (column III), of brothers and sisters (column II) and of unrelated individuals (columns I and V). In columns I–III the individual values are alone considered, while in columns IV and V the quantitative values of right and left hands are noted separately

twins a coefficient of correlation is found ($r = 0{\cdot}535 \pm 0{\cdot}082$) very similar to that of single brothers and sisters. The 15 pairs of identical (?) twins give, finally, an example of a remarkably high correlation, the coefficient here amounting to $0{\cdot}924 \pm 0{\cdot}037$—a correlation, indeed, which fully equals and even slightly exceeds that found for the values of right and left hands of identical twins (column IV), $r = 0{\cdot}86 \pm 0{\cdot}027$, or of single persons (column V), $r = 0{\cdot}886 \pm 0{\cdot}039$.

Unrelated individuals	[Table XXII, column I]	30 pairs	$r = -0{\cdot}270 \pm 0{\cdot}128$
Brothers and sisters	[„ „ II]	30 „	$r = +0{\cdot}595 \pm 0{\cdot}118$
Fraternal twins	[„ „ III]	16 „	$r = +0{\cdot}535 \pm 0{\cdot}082$
Identical twins	[„ „ IV]	15 „	$r = +0{\cdot}924 \pm 0{\cdot}037$
Hands of identical twins	[„ „ IV]	30 individuals	$r = +0{\cdot}860 \pm 0{\cdot}027$
Hands of single persons	[„ „ V]	30 „	$r = +0{\cdot}886 \pm 0{\cdot}039$

TABLE XXIII. Coefficients of correlation for the pattern-values of pairs of individuals and of right and left hands.

A correlation between the pattern-values of identical twins, as here demonstrated, very strongly supports the assumption of the quantitative value of the finger-patterns being an hereditary character.

The result of a comparison of the correlation between pairs of identical twins with that between right and left hands is further in perfect agreement with the view maintained by Newman that in a pair of identical twins each individual represents, as it were, one side of the original system of symmetry. While for the more vital organs a new system of symmetry has been developed within each twin, the original symmetry seems to have been kept with regard to the finger-patterns, in the same way as it has, according to Wilder, also been kept with regard to the general existence of papillary patterns upon the whole palms.

With regard to the design of the finger-patterns, our twin material, again, fully supports the view held in this paper of its being determined through two independent, hereditary characters (factors, or group of factors), namely, in the first place the circular or the elliptic shape of the pattern, and in the second place the regular, approximately concentric development of ridges, opposed to the tendency to twist. Within the, presumably, identical twins each of the two members of a pair have always either both a circular pattern-shape (eight cases), or both have elliptical shapes (three cases), while in four pairs both members have a median shape. In the same way the tendency to twist occurs, if present, always in both members of a twin-pair, in three pairs combined with a circular pattern-shape, in two others with an elliptical one, and in four pairs, finally, with a median shape of the patterns. In the remaining

six pairs the development of the patterns is regular. It should in this connection be remembered, that a correspondence of the pattern-design is often found also among ordinary sisters and brothers, it is therefore not at all surprising to find it among twins. The constancy of correspondence, however, within the whole group of identical (?) twins deserves here to be emphasised, especially in view of the fact that within the group of fraternal twins (16 pairs) no less than five pairs exist with essential differences of pattern-design.

It is of great interest also to look at the minor characteristics of the finger-patterns of twin-pairs. They are not at all always alike, nor indeed are those of right and left hands; but we not infrequently (three or four times among our 15 pairs) find cases in which the similarity between the fingers of the four hands is very striking.

In one twin-pair (see Fig. 14, p. 40) we find, for instance, especially upon digits I and II, in part also upon digit IV, a very interesting display of all grades of development of, as it were, one and the same pair of double loops. Both loops may be well developed, or only one of them, and even this one may (digit II) be so faintly visible, that the pattern would, in practical classification, be considered an arch. But, after all, all these patterns are so alike with regard to the whole course of the ridges that, as mentioned before, the central part of one pattern might be cut out and placed upon nearly any one of the others and fit very well into their peripheral ridges. Even the patterns of the other fingers, partly shown in Fig. 11 (p. 37), which show all stages of development between the arch and the single loop, display the same plan in the whole course of their ridges. I may add in this connection, that in my whole material of about 200 individuals, no single one exists whose finger-patterns might be interchanged with those of this twin-pair. The patterns of their father have the same main course of the ridges as found in this twin-pair; he has upon his first fingers also double loops exceedingly similar to those of Nr. 1, 13. But none of the minor characteristics displayed upon the other fingers of the twins are found in the patterns of their father.

Two other twin-pairs, the fingers of which are also strikingly alike, are shown in Figs. 36 and 37. In both pairs each right finger of one twin can be directly compared with the same finger of the other, and so also with the fingers of the left hands. Two exceptions only are found from this rule, both in the twin-pair, Nrs. 165 and 166 (Fig. 36). One is seen in digit I where the symmetry found in the other fingers is replaced by a mirror symmetry, the very characteristic double loops of the right side of Nr. 165 being found on the left hand of Nr. 166. The other exception

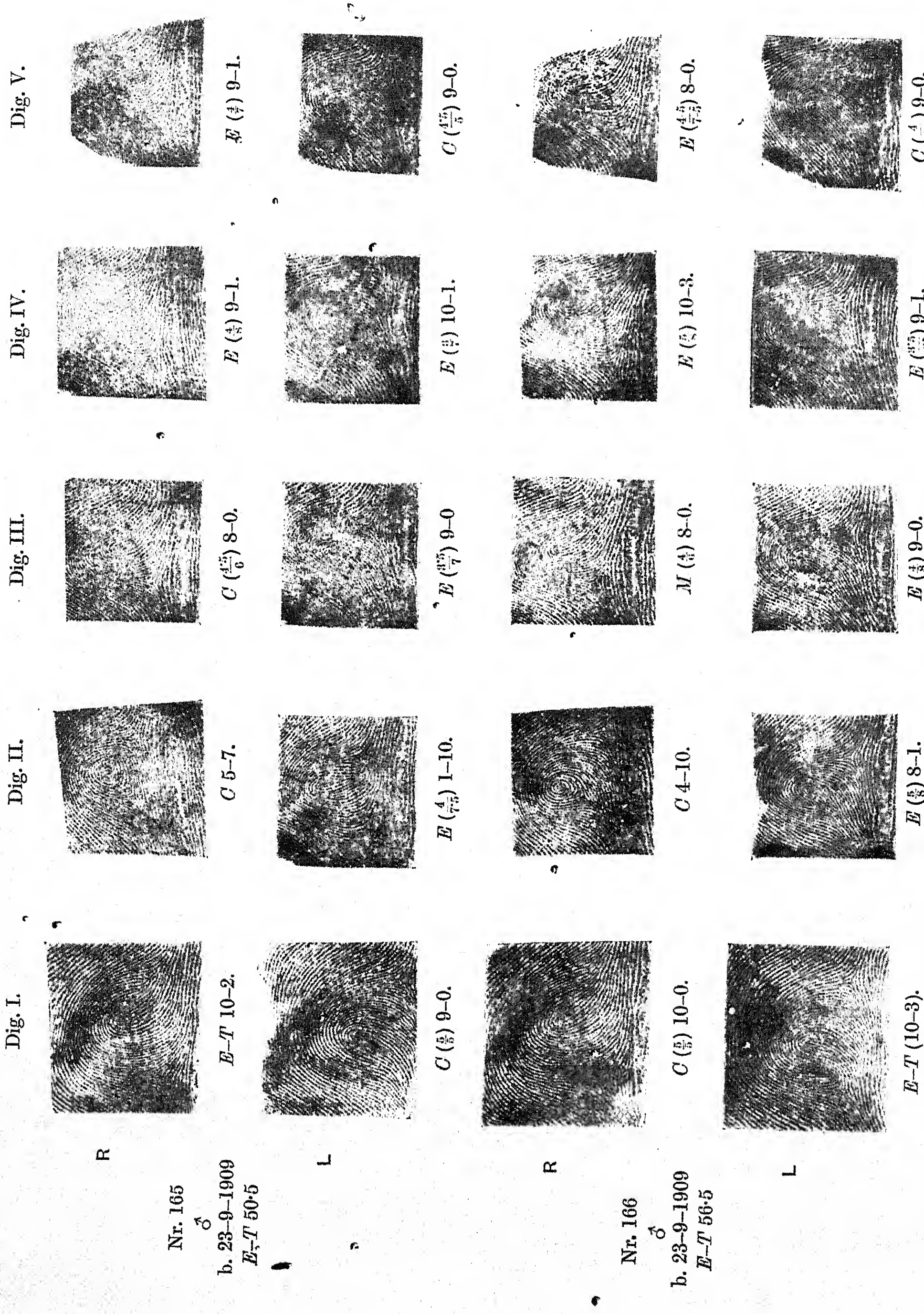


Fig 36. Finger-patterns of a pair of presumably identical twins, Nrs. 165–166.

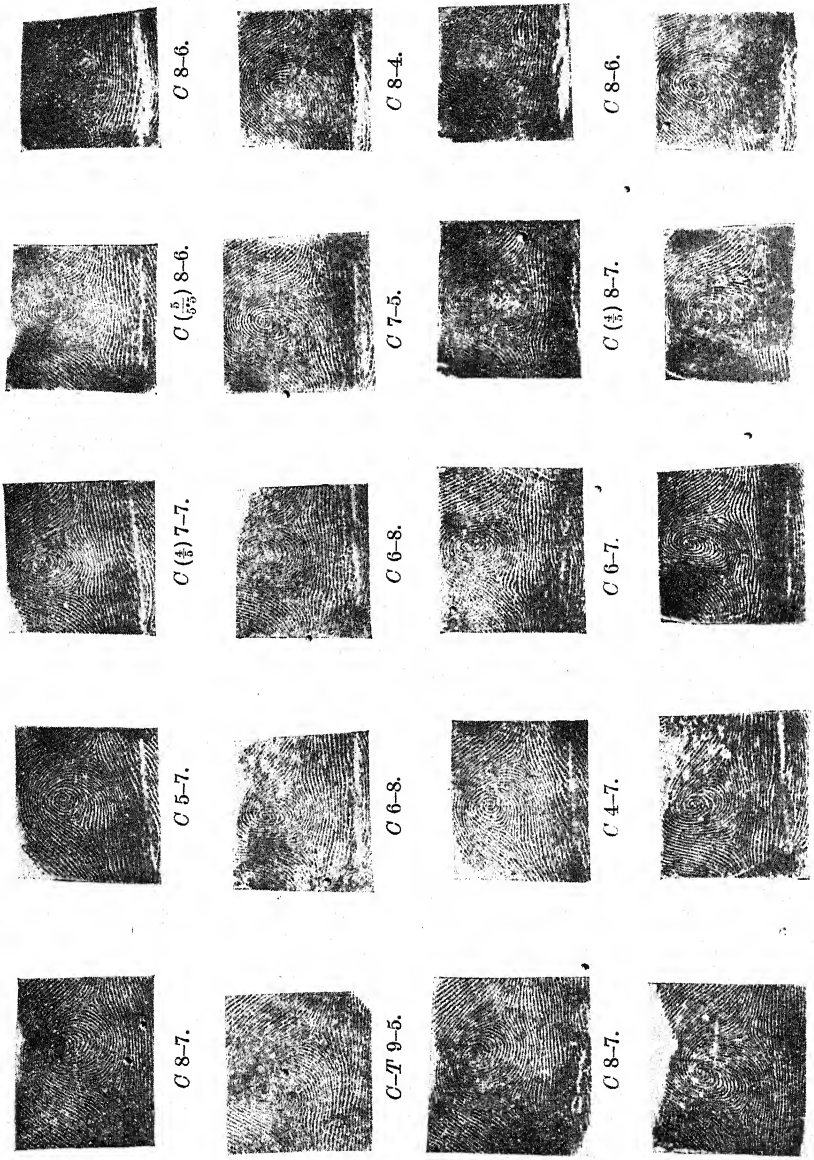


Fig. 37. Finger-patterns of a pair of presumably identical (?) twins, Nrs. 169–170.

from full symmetry is that of a reversal of the pattern from an ulnar to a radial direction upon the left digit II of Nr. 165, a phenomenon so often met with upon this finger.

On the whole the results obtained through an investigation of my twin-material have proved to be valuable not only as a control, but also as a support for the suggestions made in this paper with regard to the heredity of papillary patterns.

Before finishing I may mention that I have had an opportunity of investigating the finger-patterns of a series of polydactylous individuals, belonging to the family described by Sverdrup (1922), included in Fam. 4 of this paper.

A similar investigation has been made also by Wilder (1904) upon two individuals with a double thumb. "I had naturally expected, *à priori*," he says (p. 453), "that the patterns of the two right thumbs would prove to be duplicates of one another, but such is by no means the case."

In the five individuals investigated by me, the polydactyly was post-axial; a duplication of the patterns of digit V might, therefore, possibly be expected. My result was, however, like that of Wilder, absolutely negative, no duplication existing.

This negative result agrees very well with the view maintained in this paper of a causal connection between the shape of the finger-ball and the pattern found upon it. The extra fingers of polydactylous individuals very seldom have their balls quite normally developed, a fact which must influence the configuration of the papillary pattern.

Summary.

(1) A statistical investigation of the finger-prints of 24,518 Norwegian criminals has proved the different pattern-types to occur in the following percentage of all fingers: whorls 25·65 per cent., radial loops 5·81 per cent., ulnar loops 61·14 per. cent. and arches 7·4 per cent. Their distribution proved to be characteristic of each of the ten fingers, the whorls reaching their maximal occurrence upon digits I and IV of right hands, the arches and the radial loops upon digit II, while the ulnar loops are most numerous upon digit III and, even more so, upon digit V (see Tables I and II).

(2) A comparison with similar statistics found in literature and based on other human races proved the total numerical occurrence of each pattern-type to be characteristic of each race investigated (Table V). The distribution of each type upon the various fingers proved, however

in all races to show the same characteristics as in the Norwegian material (Tables VI–IX).

(3) A thorough analysis of the finger-patterns of *ca.* 200 individuals, showing a complete series of transitions between the pattern-types of Galton (Figs. 10–17), has, for a study of heredity, proved the necessity of finding a basis of classification which gives a more detailed expression of the design and development of each pattern, as well as of the natural relations between different patterns.

(4) The same analysis has, further, proved the existence in the phenotypical appearance of finger-patterns of three independently varying characters, the design of patterns being determined through (1) the circular-elliptical shape together with (2) the presence or absence of a tendency to twist, that is, to form double loops or their derivatives. Besides the design, the (3) quantitative value, varying independently of the two characters mentioned, is always a prominent feature of the pattern.

(5) A classification of all patterns has been based upon ridge-counting, the shape and the quantitative value of each pattern being treated separately (Chapter 5, Pls. I and II). The characteristics of each individual are, finally, determined by a consideration of those of the ten fingers (Tables XI and XII) and have, together with the quantitative values of each finger, been introduced into the pedigrees (Fig. 23, Pls. III and IV).

(6) The quantitative values of separate fingers seem within each individual to be subject to some restriction with regard to their range of variation, all having, ordinarily, either relatively low or relatively high values (Table XIII). A certain quantitative pattern-value has, therefore, been supposed to be characteristic of each individual, while the varying appearance of the patterns upon the ten fingers should be seen in causal connection with the shape of each finger-ball.

(7) This view is supported also by a comparison between the very irregular variation-curves of the quantitative finger-values (Figs. 24–27), and the approximately symmetrical curve of individual values (Fig. 28), proving the fluctuating variation of finger-patterns to be equalised when the patterns are grouped as belonging to separate individuals.

(8) The variation curve of individual values (Fig. 28) proves the very low as well as the very high values to be of rare occurrence; heredity of the quantitative value is, therefore, indicated by the fact that nearly related individuals have been found to have such rare values.

This assumption of heredity is further supported through a con-

sideration of a series of family groups, graphically represented in Fig. 29 *a–b*.

The relation between the values of parents and children within each of these groups, together with the symmetrical curve formed by the values of the whole population (Fig. 30, Tables XIV–XVI), indicates the type of heredity to be one based upon multiple factors.

(9) The circular (C)-elliptic (E) shape of finger-patterns as well as minor characteristics have, by an analysis of pedigrees (Fig. 23, Pls. III and IV, Table XVII) and patterns (Figs. 31–34), proved to be hereditary. The mode of inheritance could not be definitely decided, although it seems not improbable that E and C represent a pair of allelomorphs (factors or factor-groups), and that E is the dominant.

(10) The tendency to twist (T), which ordinarily is found most fully developed upon digit I (Tables XVIII and XIX), has in the same way (Table XX) been proved to be hereditary. Although the mode of inheritance could not be definitely decided, indications exist that T is dominant over R the regular, untwisted condition.

(11) With regard to the direction of finger-patterns no heredity has as yet been demonstrated. The ulnar direction is by far the most common, while on digit II a reversal to a radial direction is very often found (Table XXI).

(12) An investigation of the finger-patterns of twins, among which 15 pairs are considered identical, has upon all points supported the views here maintained with regard to the heredity of the quantitative value as well as of the whole design of finger-patterns (Figs. 35–37).

The coefficients of correlation for pattern-values (Tables XXII, XXIII) prove the correlation between the values of identical twins to equal that between the values of right and left hands of single individuals.

(13) In polydactylous individuals the pattern of the extra finger was not found to be a duplication of the neighbouring finger.

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Dig.	H	Corr. Fact.	0,5	1	1,5	2	2,5	3	3,5	4	4,5	5	5,5	6	6,5	7	7,5	8	8,5	9	9,5	10
I	r	0,86	0,43	0,86	1,29	1,72	2,15	2,58	3,01	3,44	3,87	4,30	4,73	5,16	5,59	6,02	6,45	6,88	7,31	7,74	8,17	8,6
	l	0,98	0,49	0,98	1,47	1,96	2,45	2,94	3,43	3,92	4,41	4,90	5,39	5,88	6,37	6,86	7,35	7,84	8,33	8,82	9,31	9,8
II	r	1,00	0,5	1	1,5	2	2,5	3	3,5	4	4,5	5	5,5	6	6,5	7	7,5	8	8,5	9	9,5	10
	l	1,08	0,54	1,08	1,62	2,16	2,70	3,24	3,78	4,32	4,86	5,40	5,94	6,48	7,02	7,56	8,10	8,64	9,18	9,72	10,26	10,8
III	r	1,17	0,58	1,17	1,75	2,34	2,92	3,51	4,09	4,68	5,26	5,85	6,44	7,02	7,61	8,19	8,78	9,36	9,95	10,53	11,12	11,7
	l	1,10	0,55	1,10	1,65	2,2	2,75	3,3	3,85	4,40	4,95	5,5	6,05	6,6	7,15	7,7	8,25	8,8	9,35	9,9	10,45	11,00
IV	r	0,80	0,4	0,8	1,20	1,6	2,0	2,4	2,80	3,20	3,6	4,0	4,4	4,8	5,2	5,6	6,0	6,4	6,8	7,2	7,6	8,0
	l	0,86	0,43	0,86	1,29	1,72	2,15	2,58	3,01	3,44	3,87	4,30	4,73	5,16	5,59	6,02	6,45	6,88	7,31	7,74	8,17	8,6
V	r	1,25	0,62	1,25	1,88	2,50	3,13	3,75	4,38	5,00	5,63	6,25	6,88	7,50	8,13	8,75	9,38	10,00	10,63	11,25	11,88	12,50
	l	1,15	0,58	1,15	1,72	2,30	2,87	3,45	4,02	4,60	5,17	5,75	6,32	6,90	7,47	8,05	8,62	9,20	9,77	10,35	10,92	11,5

TABLE XXIV. Table of multiplication used for correcting the quantitative values. The corrected value is obtained by finding on this table the figure belonging to the horizontal line of the finger in question, as well as to the vertical column of the quantitative value to be corrected.

EXPLANATION OF PLATES.

Pls. I, II. Examples of classification of finger-patterns (see Chapter 5).

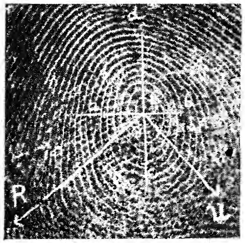
On the patterns. C, centre of the pattern; R, radial; U, ulnar side of the finger; a–b, breadth, c–d, height of the pattern.

Below the patterns. r, number of ridges between triradii and centre, the first figure representing the radial side of the pattern; v, quantitative value of the pattern, determined as the medium between the two class-values of the pattern-sides; $\frac{B}{H}$, shape-index, meaning the relation between breadth and height of the pattern, both expressed in mm. According to the size of this relation the pattern-shape is characterised as C, circular; E, elliptic; or M, median. Twisting tendency of the ridges is expressed by a T besides the C, E or M.

Pls. III, IV. Pedigrees showing the design and quantitative value of finger-patterns of individuals belonging to Fams. 1, 2, 4, 5, 6, 7.

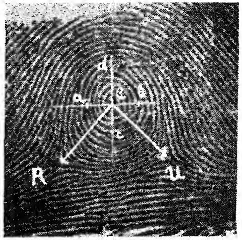
For each person the individual characteristics are noted (underlined); below this line the quantitative values of all ten fingers are noted in two vertical columns, the first column representing the fingers of the right hand, the second column those of the left. Within each column the values of digits I–V are noted in a series from above downwards. Below the class-values of the finger-patterns, finally, a figure is found in brackets; this is the "uncorrected" quantitative value of each individual (cf. p. 55).

The numeration of individuals is within all the pedigrees carried out according to the decimal-system used in "Inst. f. arv. forskning" of the University of Kristiania (see Sverdrup, 1922, p. 218).



$r: 19\text{–}14;\ v: 9-8=8{\cdot}5 \,\Big|\, \frac{B}{H}:\frac{16}{20}=C$

$r: 15\text{–}15;\ v: 8-8=8 \,\Big|\, \frac{B}{H}:\frac{11{\cdot}5}{18}=E$



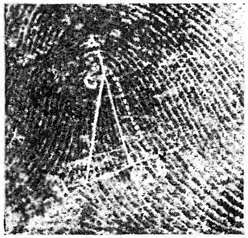
$r: 13\text{–}14;\ v: 7-8=7{\cdot}5 \,\Big|\, \frac{B}{H}:\frac{11}{3{\cdot}5}=C$

$r: 4\text{–}7;\ v: 3-5=4 \mid C$

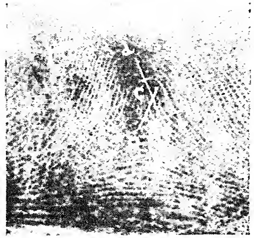
$r: 0^*\text{–}0^*;\ v: 1-1=1 \mid C$

$r: 13\text{–}18;\ v: 7-9=8 \,\Big|\, \frac{B}{H}:\frac{11}{27}=E$

$r: 20\text{–}0;\ v: 9-0=4{\cdot}5 \,\Big|\, \frac{B}{H}:\frac{10}{25}=E$



$r: 0\text{–}6;\ v: 0-4=2 \,\Big|\, \frac{B}{H}:\frac{9}{12}=E$



$r: 3\text{–}0;\ v: 3-0=1{\cdot}5 \,\Big|\, \frac{B}{H}:\frac{6}{9{\cdot}5}=E$

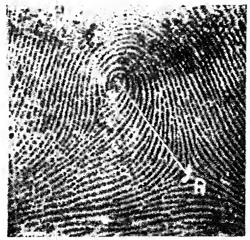
$r: 2\text{–}0;\ v: 2-0=1 \mid C^2$

$r: 12\text{–}15;\ v: 7-8=7{\cdot}5 \,\Big|\, \frac{B}{H}:\frac{15}{18}=C$

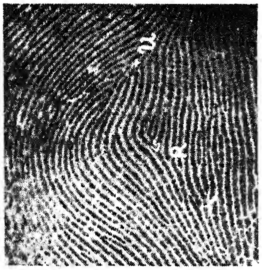
$r: 11\text{–}3^2;\ v: 7-3=5 \mid E\text{–}T$

$r: 12\text{–}2^2;\ v: 7-2=4{\cdot}5 \mid M\text{–}T$

$r: 28\text{–}1^2;\ v: 10-1=5{\cdot}5 \mid M\text{–}T$



$r: 18\text{–}1;\ v: 9-1=5 \mid E\text{–}T$



r : 0*–0* ; v : 1 – 1 = 1 | C–T

r : 5–0* ; v : 4 – 1 = 2·5 | C–T

r : 12–3 ; v : 7 – 3 = 5 | C–T

r : 8–14 ; v : 5 – 8 = 6·5 | C–T

r : 25–18 ; v : 10 – 9 = 9·5 | E–T

r : 0*–0 ; v : 1 – 0 = 0·5 | C–T

r : 15–0 ; v : 8 – 0 = 4 | C–T

r : 8–18 ; v : 5 – 9 = 7 | C–T

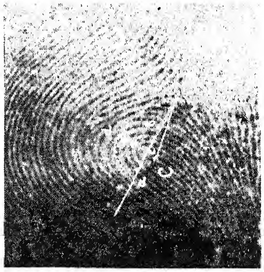
r : 13–1 ; v : 7 – 2 = 4·5 | C–T

r : 19–12 ; v : 9 – 7 = 8 | C–T

r : 0–0 ; v : 0 – 0 = 0 | C

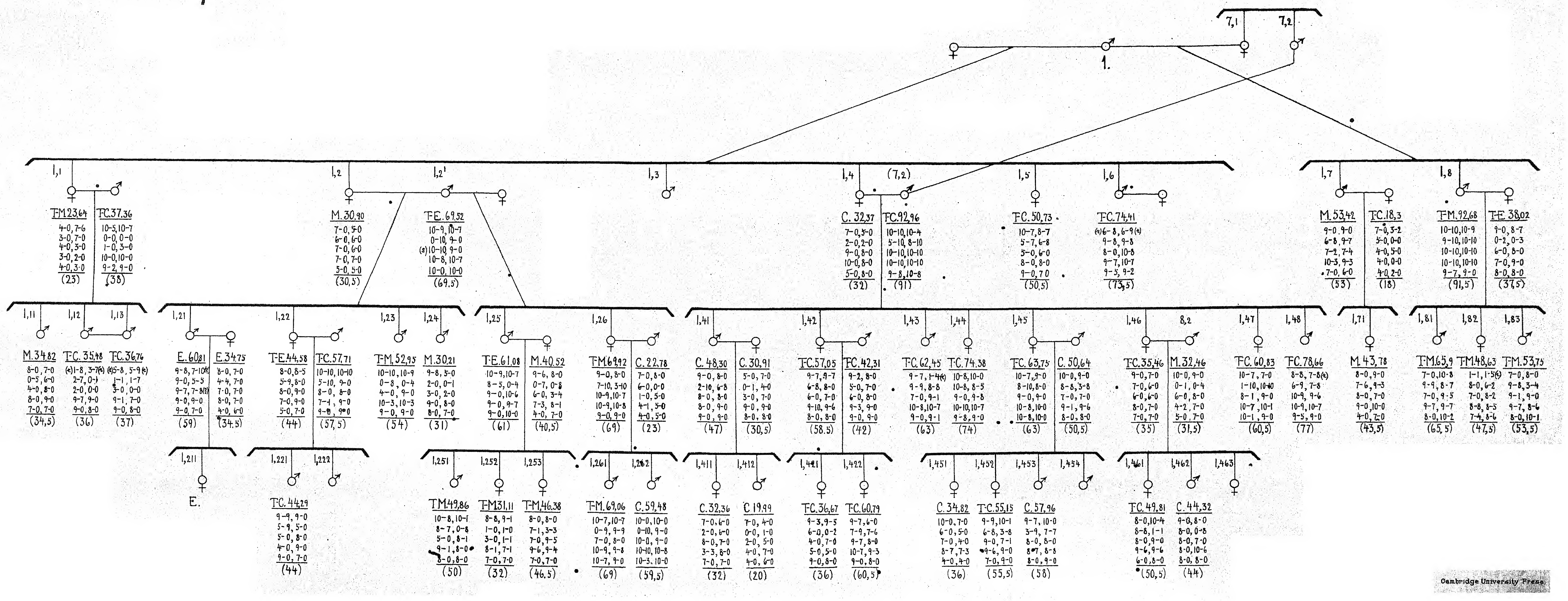
r : 2–0 ; v : 2 – 0 = 1 | C

r : 6–0 ; v : 4 – 0 = 2 $\left|\ \frac{\mathrm{B}}{\mathrm{H}} : \frac{9}{9} = \mathrm{C}\right.$



r : 0–11 : 0 – 7 = 3·5 $\left|\ \frac{\mathrm{B}}{\mathrm{H}} : \frac{12}{6} = \mathrm{C}\right.$

r : 19–0 ; v : 9 – 0 = 4·5 | C



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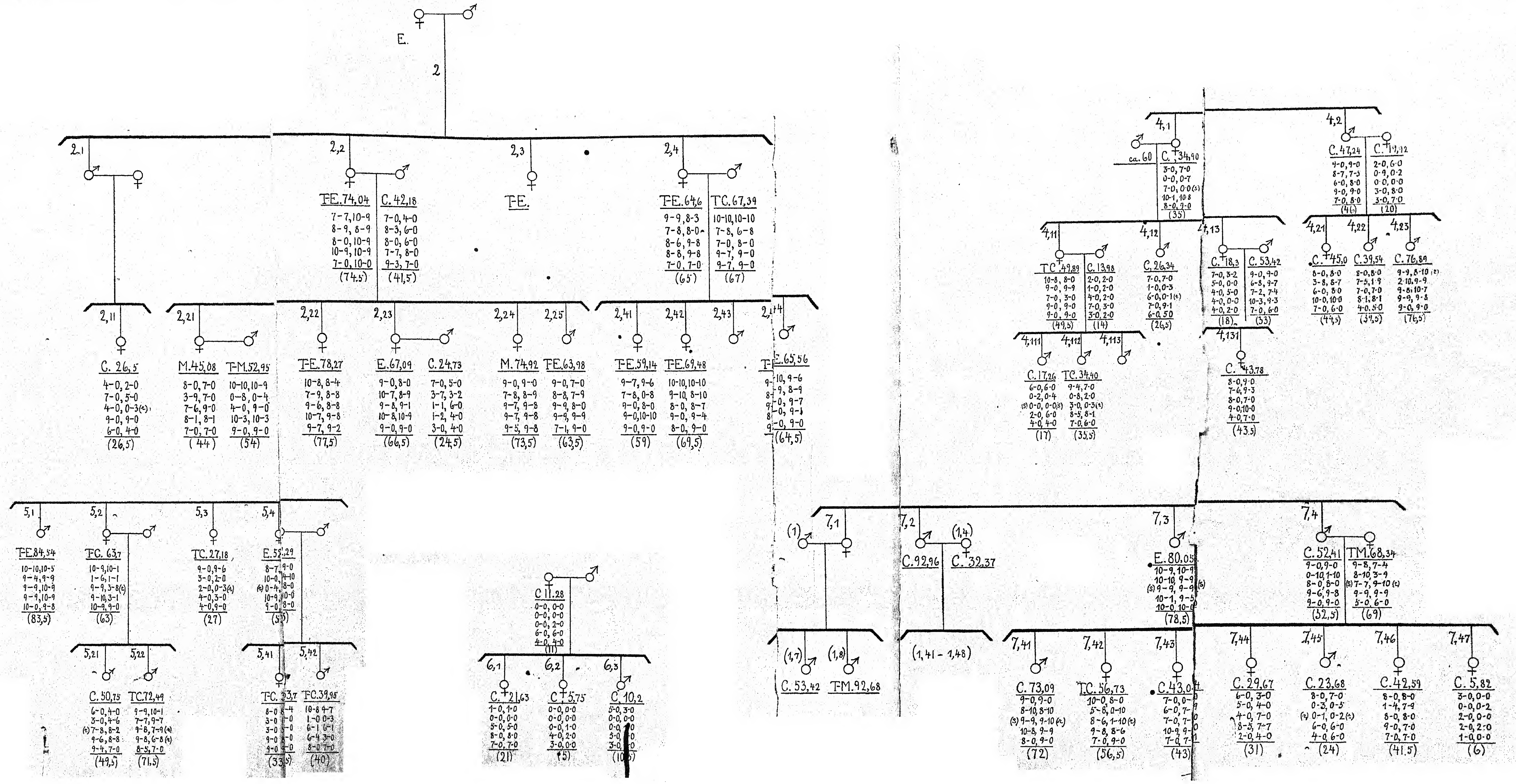
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T-M.52,95
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T-E.69,48
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THE INHERITANCE OF INVERSE SYMMETRY IN *LIMNAEA PEREGRA*.

BY CAPTAIN CYRIL DIVER, M.A.,

ASSISTED BY

PROF. A. E. BOYCOTT, D.M., F.R.S.,

AND

MISS SYLVIA GARSTANG, M.A.

(*From University College Hospital Medical School, London.*)

(With Plate V and Six Text-figures.)

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1. Introduction.

The experiments with which this paper deals were initiated by Boycott in 1920 with four young sinistral individuals of the normally dextral species *Limnaea peregra* (Pl. V, figs. (*a*)–(*h*)). These animals were originally derived from the mixed (dextral and sinistral) population of the well-known King Lane pond near Leeds, and had been reared in Mr J. W. Taylor's aquarium, by whom they were kindly given to Boycott. One pair was bred at first at Radlett, the other in London at University College Hospital Medical School, where most of the subsequent breeding has been carried out. By the time that the second generation had been obtained it became evident that the only hope of solving the problem of the inheritance of sinistrality lay in mass production beyond the powers of one individual.

To this end, as stated in our preliminary paper (Boycott and Diver, 1923), the cooperation was secured of a number of other workers, to whom our thanks are due for placing at our disposal the full records of their work. From the nature of this enquiry, the suggestions I have to offer in the following pages must be of a tentative character, and it is therefore obviously of great importance that the full results should at the same time be presented in their proper genealogical sequence. The pedigree tables (I–VI) here given embody all the results obtained by all workers up to the end of the 1923 breeding season. We are particularly indebted to Dr F. M. Turner for help in breeding.

2. General Problem of Inversion.

As the organization of an individual follows a regular pattern typical of the species or genus to which it belongs, it is clear that one of the

possible variations may be the complete inversion of this pattern. Thus an individual may result with a form precisely similar to that typical of the species in every respect but one, namely, the relation of its distribution to a median line or plane of symmetry. Such an individual is nothing more than a mirror-image of the typical form. It is obvious that when the structure is almost symmetrical about the median line such a variation would in practice be imperceptible; hence, from a genetical standpoint, the behaviour of this type of variation can only be adequately analysed in forms which present an external and easily recognizable asymmetry. These conditions are perhaps better fulfilled in gastropods than in any other form. Total inversion in this group is not only immediately recognizable in practically every case by the direction of the shell spiral, but can also be determined from the anatomy.

If, when we look from above at the apex of a gastropod shell, the spiral grows from the apex or centre outwards in a clockwise manner the shell is said to be dextral (Pl. V, figs. (*a*), (*c*), (*e*), (*g*)). If the spiral grows in an anti-clockwise manner the shell is said to be sinistral (Pl. V, figs. (*b*), (*d*), (*f*), (*h*)). That is, if the shell is held with the aperture facing the observer, the aperture in dextral shells is on the right and in sinistral shells on the left.

The majority of gastropods are typically dextral in pattern, but many genera, *Physa*, *Clausilia*, etc., are typically sinistral. Other genera, *Gastrocopta*, *Columna*, *Cochlitoma*, etc., though mainly composed of dextral species, contain one or more that are typically sinistral. The reverse position is exhibited in the genus *Fauxulus*. Other genera include many species that freely display both forms within the limits of the species (amphidromic); the two types may be found living together in a single colony or separately in different areas of their distribution, *Achatinella*, *Partula*, etc. Such genera not only include species that are freely amphidromic but others which are constantly dextral or constantly sinistral. Pelseneer (1920) has shown that there is a complete series containing a full range of possibilities between the "odd," or sporadic, sinistral individual found here and there, but very rarely, in a typically dextral species, and the "odd" dextral similarly found in a sinistral species[1]. (For the detail of this series the reader is referred to Section 30 and the full discussion in Pelseneer's book, pp. 732 *et seq.*)

In all these forms inversion is complete.

In a few genera this proposition does not hold good. The spiral appears

[1] For brevity the term "odd" is throughout used to denote occasional individuals of a form the contrary of that prevailing in the great majority of any family or population.

to be dextral while the anatomy of the soft parts is sinistral (*Planorbis*, etc.) or *vice versa* (*Limacina*, *Lanistes*, etc.). Such a condition is known as hyperstrophy (Cooke, 1895; Taylor, 1894–1900). This may perhaps best be exemplified by the genus *Planorbis*, which is shown by its anatomy to be a typically sinistral genus while the spiral *appears* to be dextral merely because the centre or true apex of the shell has been, as it were, "pushed through" itself until it has emerged on the other side. This condition is not known in *Limnaea* unless possibly the abnormal flat-coiled shells of the type shown in Pl. V, figs. *k* i–iv may be referred to it.

It need hardly be pointed out that complete inversion is not confined to molluscs, but is a well-known fact in many groups including Man, where it appears as a complete transposition of the asymmetrically arranged viscera. From the point of view of tracing its onset and possible cause, gastropods are again perhaps among the most suitable material, for they, in common with annelids, and a few other groups, exhibit the so-called spiral type of cell cleavage.

In 1894 Crampton, working on *Limnaea columella* and *Physa heterostropha*, was able to demonstrate that from the second cleavage onwards the development of the eggs of the sinistral *Physa* was a mirror-image of the development exhibited by the dextral *Limnaea*.

Kofoid (1894), working on *Limax*, pointed out the same thing.

Conklin's (1897) work on the dextral *Crepidula* demonstrated that the spiral character of the cleavage began with the *first* division, which in this case was dexiotropic, the subsequent divisions following in regular alternation up to an advanced stage; the first thus setting the direction of all subsequent divisions.

To-day there can be no doubt that a causal relationship exists between the inversion of the cleavage pattern of the egg and the inversion of the final asymmetry of the adult. Moreover, since it is clear from the position in nature that inversion is a condition which in most, and I hope to show in practically all, cases must obey some definite law of heredity, the factors governing this condition must be resident in the germ-cells themselves.

Thus we are faced with a character with two very sharply distinguished types of appearance; the development of which brings about a complete and deep-seated change in the whole organization of the individual; which in certain cases may create a very definite barrier to the cross-fertilization of individuals or races of opposite appearance; which in spite of this may be found not only as a definite specific characteristic but also

arising as a local race within the confines of a single species or even as a sporadic and apparently non-hereditary mutation throughout many forms of life; a character most definitely not the product of experimental interference.

Under these circumstances no theory of the mechanism by which such a character is transmitted can seriously be entertained which does not embrace all forms of total inversion whether definitely hereditary and racial or apparently non-hereditary and sporadic.

Though *Limnaea peregra* is one of the commonest and most abundant fresh-water snails in Britain, reversed examples are very rare. With the kind assistance of Mr J. W. Taylor, who has placed his collection of records at our disposal, we can give the following list: it is doubtless incomplete.

(i) *Localities in which a number of specimens have occurred, in some cases over a number of years.*

Surrey. Pond in a field at Tooting. First found by S. C. Cockerell (1886) in 1885 who, in the course of three or four years, got about 50 sinistral specimens. Pond now destroyed; a specimen in the British Museum.

Durham. Pond near the vicarage at Monk Hesleden. First found by Canon Tristram about 1870; seen by C. T. Trechmann (1906) in 1895 but not again till 1903; about 1911 W. Bateson (1913) estimated the proportion of sinistrals at about 3 per cent.

Yorkshire. Valley Pond, Scarborough. Many found by Alderman William Bean (1834) about 1833; specimens in the British Museum. King Lane pond[1], Moortown, Leeds: first found by W. Nelson (1901) in 1901; still living there. Proportion of sinistrals estimated by J. A. Hargreaves (1919) in 1916 as between 1 and 2 per cent.; by W. H. Hutton (in litt. 1924) as 1 in 30 at present, though formerly 1 in 5. In June 1924, with the help of Mr Greevz Fysher we found 81 dextrals and 3 sinistrals.

(ii) *Sporadic examples.*

London. Specimen sent by J. Pickering to Mr Taylor in 1864 labelled "London."

Devon. Donovan (1802) records and figures a sinistral *Limnaea* from Devon which might be *peregra* or *palustris*.

[1] From information obtained by Mr Fysher it appears that the King Lane pond is quite modern: fifty or sixty years ago it was a quarry hole.

Yorkshire. One found by J. Wilcock at Wakefield before 1883.

Westmorland. One in the Chara marl at Hale Moss in 1906, J. D. Dean (1907).

Glamorgan. One found by F. W. Wotton in 1889, near Cardiff.

Lanark. Found by Dr Buchanan White (1873) in 1873 near Dalmarnoch Bridge in a small stream running into the Clyde.

Shetlands. One from a pond near Balta recorded by J. G. Jeffreys (1859).

Ireland. One found by R. A. Phillips in sand dredged from River Suir at Fiddown near Waterford.

In this species, as far as we have been able to ascertain, sinistrals have always occurred with the normal dextral form and with the latter in large numerical excess. They have been found scattered throughout the country from the Shetlands to Surrey, Devon and Kilkenny in streams as well as in ponds of various kinds. Thus the pond at Hesleden is an "ordinary cattle pond" with *Planorbis nautileus* and *Pisidium "fontinale"*; the King Lane pond is rich in Mollusca (*Paludina vivipara, Planorbis corneus, Pl. complanatus, Pl. albus, Limnaea stagnalis, Sphaerium corneum*); in the Westmorland shell marl *Bithinia tentaculata* and *Valvata piscinalis* are the predominant species.

In no case have sinistral specimens of other species been found with sinistral *peregra*[1], and only in the Tooting locality have other malformations of *peregra* been recorded. Mr Cockerell here obtained, as he has been good enough to inform us, several interesting monstrosities; the one which is still preserved in the British Museum is a dextral shell with a somewhat intorted spire and a flattened outer lip.

Breeding experiments have been made by several observers. From wild adult sinistrals, the other parent, if any, being unknown (see below, p. 143), Nelson bred a mixture of dextrals and sinistrals, the sinistrals being "extremely scarce" compared with the dextrals; in some cases at any rate both dextrals and sinistrals were observed to come from the same egg mass. Hargreaves, with similar material from the same King Lane pond, got dextrals and sinistrals in the proportion of 5 to 1 and from wild dextrals only dextrals except in one instance where three sinistrals were obtained: he also obtained dextrals and sinistrals from the same egg mass. Hutton also got a mixture from wild sinistrals. Trechmann isolated a number of wild infant sinistrals and ultimately

[1] In 1909 the Rev. W. A. Shaw found 17 sinistral specimens of the closely allied *Limnaea auricularia* with a single sinistral *L. stagnalis* in Naseby Reservoir, Northants.; specimens are in the collection of Mr J. R. le B. Tomlin.

"nearly equal numbers of sinistrals and dextrals were produced, the sinistrals slightly preponderating."

A good many attempts appear to have been made to colonize the sinistrals from King Lane into other ponds in the neighbourhood but without any success. A number of similar experiments have been started with the surplus snails of the present series; the results will be reported in due course. The positions of the King Lane and Hesleden ponds have been marked on ordnance maps which have been deposited in the library of the Conchological Society in the Manchester Museum.

3. MATERIAL.

Considered as material for biological experiment, the smaller species of *Limnaea* have much to recommend them, but for genetical work they are, perhaps, less satisfactory. From the former view-point the main advantages are that, given initial care with regard to conditions, the animals require but slight attention and do not occupy an undue amount of space. The time per generation is not long and can within limits be controlled. The animals are hermaphrodite and both parents, under proper conditions, give extensive broods. On the other hand, the apparent freedom with which these snails self-fertilize (Section 5) in captivity, although valuable in the study of pure lines, may introduce a considerable source of error in experiments involving cross-breeding.

Although there is marked variation within the species under review, the characters in which it appears are mainly such that in regard to them it is difficult to rule out the possibility of environmental effects. Had we been able to follow up a single Mendelian character simultaneously with variation in symmetry, the course of this enquiry might have been less arduous. Added to this the genetical analysis of a character which involves the complete transposition of the asymmetrical organization of the individual is further hindered by the fact that, in gastropods generally, the genitalia are asymmetrically situated. In the larger land Pulmonates this fact produces a complete mechanical barrier to the crossing of individuals exhibiting opposite asymmetry. This has been made abundantly clear to me by a detailed study of the courtship and mating habits of several British *Helices* and has been experimentally verified by Lang (1896) (*Helix pomatia*) and Standen (1892) (*Helix aspersa*). In *Limnaea* the question is not answered so easily. In the larger land Pulmonates the male and female genitalia share the same opening just behind the head on the right side of the animal (in sinistral specimens on the left side). In *Limnaea* the male opening is similarly

situated, but the female opening is separated and appears further back on the same side. Further, the method of mating in *Limnaea* is not head to head as in the *Helices*, and there is consequently not a mutual exchange of spermatozoa at each copulation. The animal acting male mounts from behind the shell of the animal acting female and the penis is curved round the lip of the shell into the vagina. Copulation is not always readily or rapidly achieved. Under these circumstances only close and continued observations will determine whether any particular attempt has become an effective mating or not. When one animal is dextral and the other sinistral the animal acting male has to mount the shell of the female from the reverse position, which is readily done, and there would appear to be no unsurmountable barrier to mating. Detailed examination, however, of such attempts tends to show that this assumption is not correct. I have had two such pairs under continued observation for many days, and although frequent attempts were made throughout this period, I was never able to detect an effective mating in either case. Adams (1923) has made similar observations, though in the case of his pair it seems just possible that after very many failures a mating may ultimately have been effected. Hargreaves (1919) and Hutton (1919) record having observed such matings taking place freely in nature, but in view of the above it seems more than likely that they mistook the will for the deed.

Thus cross-breeding between animals of opposite appearance is not practicable. Fortunately the system controlling the inheritance of inversion indicated in our preliminary paper is such that this difficulty raises no real barrier to research. Under these circumstances, with the exception of the cases specifically mentioned above, whenever pairs have been used as parents, both were of the same kind, *i.e.* both dextral or both sinistral.

Another difficulty arises from the fact that the parent animals usually die shortly after the end of their first laying season, *i.e.* about October or November, while those that fail to lay, or only give a very small brood in their first season, usually live through to the next year.

This makes it difficult to obtain evidence of the effects of crossing *after* the genetical constitution of an animal has been revealed by the production of a brood without cross-fertilization. This drawback can, however, be overcome to some extent by the fact stated above that the rate of growth or time per generation can be controlled. Semper (1883), Varigny, etc., working with *L. stagnalis* found that, other things being equal, the length of the shell (*i.e.* growth) varied directly with the volume of water available. This has been found also to be the case with *L. colu-*

mella (Colton, 1908) and our experience has shown that it is undoubtedly true for *L. peregra* as well. It has been pointed out by Turner that this fact might be applied to our experiments. Thus a portion of any brood may be hurried on and the general composition of the brood determined while the remainder are held back till the next season and then paired.

This procedure has the additional benefit of being free from the danger of the long delayed action of spermatozoa which has been observed in Mollusca by von Ihering (1876) and Lang (1904). That this takes place in *L. peregra* also is suggested by the second brood derived from one of the original Radlett pair (Section 12, p. 143, and Table IV).

It is hoped that the application of this method in future work may provide further crucial tests of the general hypothesis outlined below.

4. METHOD.

In the early stages of the experiment Boycott proceeded mainly by the use of pairs. The dangers of this method, however, were soon apparent and consequently practically all the 3rd, 4th and 5th generation broods have been obtained from individuals isolated in early youth before mating could have taken place[1]. From these fertile eggs are readily obtained. This latter fact, coupled with the variations in individual growth rates, the absence of a clear external sign that sexual maturity has been reached, and the fact, found by Colton (1908) and more or less apparent from our figures, that the number of young produced is not so much related to the number of laying snails, as to the volume of water in which the snails are kept, makes it difficult to say with certainty that both parents in a pair actually did contribute to the brood. Thus of over 600 families obtained, only about 80 have been derived from pairs.

The most suitable jars were found to be of coarse greenish glass, with loose stoppers, having a capacity of about 2000 c.c. Smaller jars, such as 2 lb. jam jars, retard development or prevent the snails from reaching maturity and are useful for that purpose. They may be used also for obtaining eggs from a snail that is already adult. Jars with a larger capacity, for some reason, are not so satisfactory.

In each jar was placed a piece of *Elodea* from a source free from any possible contamination by *L. peregra*. This weed seems generally to be suitable for the healthy growth of the snails. No soil was used and dead leaves were removed, as our experience tended to show that their presence in the jar did not have a good effect.

Colton (1908) made extensive experiments as to the conditions most

[1] Such individuals put to breed alone are throughout spoken of as "singles."

suitable for the healthy growth of *L. columella* and found that dried leaves were apparently more suitable than *Elodea*. In a later paper (1918) he advocates a pinch of garden soil and one or two dried Carolina poplar leaves in filtered pond water.

Distilled water has been used for some jars, but it was found on the whole that tap water was equally suitable, *provided that the weed and water are allowed to stand in the jar for at least a fortnight before the young snail is introduced*. (For a discussion of this point, see Colton, 1912.)

The jars are kept covered with loose glass stoppers which prevent evaporation, and they are not disturbed to remove excreta or change the water. Disturbances of this sort seem to have a definitely adverse effect. As regards external conditions, by far the most successful jars are those which are placed so as to get a reasonable amount of direct sunlight. Diffused light, as in a room away from the window, or in a window with a north aspect, gives poor results. On the other hand the water temperature rapidly rises above the danger point under prolonged sunlight in hot weather. Jars in the open air exposed to the diurnal changes of temperature appear to do better than those kept in the more even temperature of a room. On these points Colton's (1908) experience appears to corroborate ours.

Clearly, from observations in nature and from the figures given by Colton (1912) of the time occupied between hatching and egg laying, it would be possible to obtain two or more generations in the year. We have so far, however, with a few exceptions, proceeded at the rate of one generation a year.

In most cases the eggs have been allowed to hatch without disturbance in the jars in which they have been laid. This method has considerable advantages, but it has the disadvantage of causing a high infantile death-rate; if the eggs are removed as laid, capsule by capsule, to fresh jars, this death-rate can be very greatly reduced.

In all cases where a snail is shown in the tables as a single, there is no question of its having been fertilized by another snail before isolation.

The broods shown have been raised by different workers under a variety of conditions. The actual distribution is revealed by turning to the reference numbers.

All broods (except a few reared by Miss Garstang in Leeds) bearing numbers from 1–800 have been bred in London or Radlett by Boycott.

Those from 2001–2200 by Mrs Bateson and myself at Merton.

Those from 3001–3100 by Mr L. E. Adams at Reigate and Stafford.

Those from 3500–3600 by Miss S. Garstang at Leeds.

Those from 4001–4200 by Mr W. H. Heathcote at Preston; Miss Rathbone at Keston; Mr Poole in the Isle of Wight.

Those from 4501–4600 by Mr T. H. Burlend at Cardiff.

Those from 5001–5200 by Dr F. M. Turner in London.

Those from 6001–6100 by Mr H. G. Thornton at Northampton.

Wherever bred, the results were concordant: there was no evidence that the differences in environment at the different places had any influence on the types of broods produced.

The soft parts have not been dissected in all cases: in a good many instances they were not available owing to the death of the snail not having been immediately observed. Samples of all the groups have, however, been examined. The anatomy of the animal has always followed the twist of the shell and, as might be expected from their normal growth and reproduction, the adult sinistrals have nothing grossly abnormal in their structure apart from the inversion of symmetry.

5. Problem of Self-fertilization.

It has been stated by us (1923) that we inferred that the fertile eggs readily obtained from isolated animals—here referred to as *singles*—were the product of self-fertilization. It has already been shown that there is no question of their being the result of cross-fertilization, as all singles have been isolated before any chance of pairing could arise. The number of broods successfully reared in this way and the number of young per brood shown in Tables I–VI give a fair impression of the abundance with which fertile eggs are laid by singles. The largest brood obtained by us was from a single, DS 509 (Table II), which gave 792 young in one season. There are indications that singles do not lay till late in the season, as it were as a last resort; but the evidence so far cannot be regarded as significant.

This state of affairs is not peculiar to *L. peregra*. Colton (1918) has found that nine other species taken from the four genera *Limnaea*, *Planorbis*, *Physa* and *Ancylus* behave in the same way. And in the case of *L. columella* he has carried a line through 31 self-fertilized generations. Similar facts are reported by various authors for further species of *Limnaea* and *Planorbis* and the records quoted by Pelseneer (1920, p. 243) embrace species of *Arion*, *Limax*, *Hyalinia*, *Zonites* and a single case among the *Helices* (Lang, 1912). Künkel (1912), working on the two slugs *Arion empiricorum* and *Limax cinereo-niger*, showed that both species produced eggs as freely from isolated singles as from pairs. The behaviour of the *Helices* is different. In his long experience of various

species from this group, Lang only records one case (1912) in *H. hortensis* where an isolated single succeeded in producing fertile eggs. During the last four years I have had several *Helices* in isolation and have so far obtained no record of fertile eggs from a single. The experience of others has been similar.

In this genus, therefore, the event must be extremely rare. Mr A. W. Stelfox, however, informs me that in 1920 he isolated a wild *H. nemoralis*, then only half-grown; in 1921 this snail reached maturity and in 1922, having had no chance whatever of mating, laid a batch of eggs from which only one young snail hatched.

Lastly, there is the case of *Paludestrina jenkinsi*, examined in detail by Robson (1923), which, when isolated, freely gives rise to fertile eggs.

Thus a considerable body of evidence is accumulating which shows that, at least in several genera of molluscs, cross-fertilization is not the only means of propagation. Whether the eggs produced in the absence of that process are due to parthenogenesis or to self-fertilization is by no means clear, but an epitome of the evidence may be given.

Pelseneer (1920, p. 243) seems inclined to ascribe these cases to "parthénogenèse naturelle" rather than "auto-fécondation": but apart from the possibility of parthenogenesis induced by copulations between different species, the evidence for parthenogenesis in Mollusca seems to rest mainly, if not entirely, on the case of *Paludestrina jenkinsi*, and there appear to be good grounds for regarding this as a special case. The near relatives of this snail are all dioecious but in this particular species no males have ever been recorded and Robson (1923) finds no trace of spermatozoa in the reproductive organs of the female.

The facts in the other cases are very different. The animals are monoecious. The sperm and eggs originate in the common hermaphrodite gland and pass from it down a common duct as far as the albumen gland which then divides into a vas deferens leading to the penis, and an oviduct at the base of which opens the blind passage of the receptaculum seminis. In *Helix* and allied genera the male and female genitalia share the same opening. In *Limnaea* and allied genera the male and female openings are separated. In the former case I am convinced from numerous direct observations that self-fertilization by means of self-copulation, if not mechanically impossible, must be extremely difficult. In the latter case these mechanical difficulties do not seem to be present: but in his considerable experience Colton (1912) states he has never observed self-copulation. My experience has been the same. Although on more than one occasion various indications have led me to

suspect that it might be about to occur, detailed observation has always so far shown that my suspicions were ill-founded. The sole evidence in support of this method of self-fertilization must therefore still rest on the single much-quoted observation made by von Baer (1835) on *L. auricularia*.

The only other possibility is self-fertilization by some internal mechanism. From the general organization of the genitalia in hermaphrodite snails it seems surprising that internal self-fertilization is not more common than it appears to be. In certain small species in hermaphrodite genera it has been shown by Steenberg (1917), Boycott (1917 *a* and *b*) and Watson (1920 and 1923) that the male organs may always (*Achanthinula lamellata*) or often (*A. aculeata*, *Vallonia*, *Vertigo*) be entirely absent; in spite of this both eggs and spermatozoa are produced in the same individual. Such phenomena are at least suggestive.

Direct evidence from cytological work is not as yet very extensive, but the following points have been put forward.

(*a*) Colton (1918) found in *L. columella* that sperm and eggs were ripe at the same time in the ovotestis.

(*b*) Künkel (1912 and 1916) showed that in the eggs of isolated *Arion* and *Limax* immediately after laying the first *and second* polar bodies were thrown out. Colton (1918) has corroborated this in *L. columella*. In normal parthenogenetic development this does not occur (Wilson, 1906, pp. 280–284) and the exceptional cases reviewed by Doncaster (1920, pp. 124–139) do not seem to be here in point. On the other hand, Pelseneer (1920, p. 674) has found in three species of *Limnaea* that in the eggs laid *after copulation with a snail of a different species* only *one* polar body was thrown out.

(*c*) Künkel (1912) has found in *Arion* that the animal's own sperm is transferred to its own receptaculum seminis. On the other hand, Colton (1912) states "into the oviduct near its aperture opens the duct from the so-called sperm receptacle, in which the writer has never found sperm but in which very often he has found eggs."

(*d*) Kleiner (1912) has demonstrated in *Helix hortensis* the occurrence of a modification of the reproductive organs by which the vas deferens is connected up with the receptaculum seminis, thus short-circuiting the passage of the sperm. Ramanujam (1922) has found a similar modification in *Veronicella*.

From *L. peregra* itself we have as yet no direct evidence to offer.

Lastly there is the indirect evidence of the genetical behaviour of

external characters. In Künkel's (1916) work on *Arion*, colour-characters in broods derived from singles appear to segregate in the normal manner.

Lang (1911) found by crossing certain *Cepaea* species that young were produced showing maternal characters only. He assumed from the evidence before him that self-fertilization was not in question, but that cross-fertilization had induced parthenogenesis, the foreign sperm acting merely as an incentive to the development of the egg but taking no part in the development of the characters. However, he found that in two cases these "hybrids" showed indications of a segregation in regard to the characters of the maternal species, indicating that the mother was heterozygous.

Baltzer examined the cytology of some of these "one-sided" hybrids and found that they exhibited practically the same chromosome number as Kleinert (1909) showed was possessed by *hortensis*, viz. diploid 46, haploid, on the average, 23 (*hortensis* having normally 48 diploid). The maturation division took place in the observed *hortensis* manner.

With this evidence before him Lang (1912) came to the conclusion that his original suggestion of induced parthenogenesis was an error and that the real explanation was to be found in the fact that induced self-fertilization had actually taken place.

The alternating system of inheritance revealed by our experiments with isolated singles would be difficult to explain on the assumption of normal parthenogenesis, whereas it can be readily understood on a system under which both sperm and ova co-operate in the transmission of factors.

6. Data Available.

In our preliminary paper (Boycott and Diver, 1923) we outlined briefly the types of broods obtained by us and the manner in which these types were found to be distributed in groups of broods derived from a common grandparent, *i.e.*, first-cousin groups. At that time we had records for about 200 broods containing over 16,000 young. The data now at our disposal and shown in the pedigree Tables I–VI include records of over 600 broods and about 53,000 young. This increase in our information not only has confirmed the general proposition put forward by us, but also seems to justify the publication of the detailed analysis upon which this proposition was founded.

To summarize, we found that all the broods obtained could at once without doubt be placed in one of six classes in accordance both with the

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appearance of the young snails contained in the broods, and the manner in which they are disposed in regard to other related broods. These brood types are:

A	B	C	D
All dextral	3 dextral to 1 sinistral	1 dextral to 1 sinistral	All sinistral
E			F
Mostly sinistral with a few odd dextrals			Mostly dextral with a few odd sinistrals

All six types may be obtained from sinistral as well as from dextral parents.

Brood types *E* and *F*, which in our previous paper were referred to as *E* (*b*) and *E* (*a*) respectively, constitute the special problem of what I have called "*suppressed*" inheritance and their significance will be discussed in later sections of this paper (see particularly Sections 18 and 28). In this and the immediately following sections the discussion will be confined to the mechanism of "normal," *i.e.* unsuppressed, inheritance.

When at the end of the 1922 breeding season the records were collected together, it was found that, although all four types *A*, *B*, *C* and *D* could be obtained from pairs, only types *A* and *D* could be obtained from singles. This result at once suggested the possibility that the asymmetry of the individual might be determined by some mechanism resident either in the spermatozoon or in the unreduced egg, or both. Determination by the egg, which seemed on the general evidence not unlikely, would lead to a more or less simple type of maternal inheritance. Such a system, however, in its simple form could not be reconciled with the possibility that the type *B* broods were real 3 : 1 broods in the Mendelian sense. In view of the suggestive, though inconclusive, nature of the evidence on this point, discussed in detail below, we did not feel justified in putting forward the very attractive interpretation since proposed by Sturtevant (1923). He suggests, in the absence of the actual figures, that the *B* broods might be regarded merely as fortuitous variants of the type *C* ratio. This suggestion is more acceptable than it might appear since we know, almost for certain, that in a type *C* brood the dextrals are deposited by one parent and the sinistrals by the other. Thus the variations of the ratio may be very considerable, *but they should be compensating* and 1 : 3 broods, which incidentally are absent, should be at least as frequent as 3 : 1.

Beyond the behaviour of dextrality in a "mixed" (type *B*) brood there appears to be no evidence of dominance. If we assume with Sturte-

vant that dextrality invariably dominates sinistrality, it would not be possible to form the expectation indicated in our previous paper, and since realized, that a sinistral isolated single can give an all sinistral (type *D*) brood, containing some individuals which, again by self-fertilization, will, in the next generation, give an all dextral (type *A*) brood (*e.g.* Table III, SS 12).

7. General Hypothesis.

From this brief review of the salient features of the problem of "normal" inheritance, I propose to turn now to the consideration of the general hypothesis formulated by us in our preliminary paper.

We there stated that we had arrived at the following general proposition: That the appearance of an individual is not determined by its own chromosome composition directly, but is the product of the parental chromosome composition. The individual may, therefore, carry in itself any of the genetically possible combinations of chromosomes; this new chromosome composition gives a fresh product which governs only the appearance of the next generation, within which again any of the genetically possible chromosome compositions may exist.

This general proposition was based upon four main assumptions:

(i) That the factors or influences determining the final result are resident in the chromosomes.

(ii) That the chromosomes carrying these factors or influences are distributed during gametogenesis in the now generally accepted manner.

(iii) That the determination of the final result is brought about by the *combined* action of the pair or pairs of chromosomes involved (see p. 131 and fig. 1).

(iv) That the effect of this combined action or product of the nuclear composition is delayed until the next generation in its appearance.

The probable truth of the first two assumptions happily does not need further discussion to-day.

The third assumption diverges from the simple Mendelian scheme in that we are evidently not concerned with simple dominance; but it seemed to follow logically both from the hint of the presence of two heterozygous types, implicit in the case referred to at the end of the last section, and from the theoretical consideration of the nature of the variation itself.

The fourth assumption of delayed action diverges further from the simple Mendelian scheme, but again follows logically as much from theoretical considerations as from the results obtained by breeding from

isolated singles. This assumption has been accepted by Sturtevant (1923) in criticising our preliminary paper and has also been applied by him in formulating the simplified hypothesis of maternal inheritance.

Thus, if we consider the simplest case—that of an isolated hermaphrodite individual producing both eggs and sperm—we must assume that the general organization of each of the germ cells of such an individual will be definitely modified, prior to gametogenesis, by the product of the chromosome composition of that individual. Thus the germ cells will be organized, either all in a dextral or all in a sinistral manner, in such a way that, in all the gametes arising from them, this dextral or sinistral organization will be present. Since, in the case we are considering, cross-fertilization is ruled out and since the individual may be said, both on its male and female side, to be homogametic in respect of this organization, it follows that all the zygotes will be made up of similarly organized gametes and will therefore themselves be similarly organized. Hence the cleavage pattern of all the fertilized eggs and consequently the final asymmetry of all the young snails of the 1st generation will be of the same type.

Now although the parent individual may be said to be homogametic in respect of this organization, *i.e.* the product of the parental chromosome composition which we have called the appearance-determiner, it does not follow therefrom that it was homozygous in respect of the factors carried by the chromosomes. Assuming that in this respect it was heterozygous it would therefore be heterogametic both on the male and female side. Consequently, if only one pair of factors is involved, four types of nuclear composition will be covered under the similar appearance of the 1st generation brood. These four types of nuclear composition will themselves form products which again will determine the general organization of the new germ cells that will ultimately become the individuals of the 2nd generation.

In the above discussion the case has been stated as if the organization both of the male and female gametes were equally affected. So far as the evidence that may be derived from breeding with isolated singles is concerned, the results would be the same whether the male cells only, the female cells only, or both male and female cells equally were affected. Which of these three alternatives is in fact operative can only be discovered by carefully controlled experiments with pairs. For these reasons we were careful to avoid restricting the issue and have stated it in its broadest terms; thus designedly we used the non-committal expression "parental."

8. Symbolical Representation of General Hypothesis.

In reducing the general hypothesis to a symbolical system which will express any individual both phenotypically and genotypically it is necessary to cover three features:

(1) The actual appearance of the individual, *i.e.* whether it has a dextral or sinistral form.

(2) Its nuclear composition in terms of chromosomes.

(3) The product of this nuclear composition (the appearance-determiner) which will control the form exhibited by its offspring.

Throughout our work we have found it advantageous to make a colour distinction between the two types of appearance under consideration; thus in the pedigree tables at the end of this paper all animals of a *dextral* appearance are shown in *red*, all animals of a *sinistral* appearance in *black*. In the following sections, when it is necessary to indicate the appearance of an individual, a *dextral* appearance is shown by the use of *heavy type*, a *sinistral* by the use of *thin type*; when the actual appearance is of no account ordinary type has been used. The nuclear composition may be shown by drawing a chromosome with its ends bent to the right or left as the case may be. As for the present we have assumed that only one pair of chromosomes is involved, the nuclear composition of all types may be shown as follows:

((indicates a pure dextral nuclear composition,
)) indicates a pure sinistral nuclear composition,
while () and)(indicate heterozygous compositions.

The product of these nuclear compositions is the appearance-determiner of the next generation and may be expressed by the use of the letters:

R (right handed)	L (left-handed)
RL (weak right)	LR (weak left).

It must be clearly understood that these letters do not denote factors in the meaning usually applied to that word in Mendelian literature, but they express the *resultant* of the *combined* action of such factors. The letters R and L may thus best be visualized as standing for two equal and opposite forces.

The simple case of a homozygous isolated single may be expressed as follows. When two ((chromosomes meet and the egg begins to develop, the resulting snail may appear as a dextral or as a sinistral according to the organization imposed upon the developing egg by the parental

appearance-determiner, but its own nuclear composition of ((will give a product, or exert a force, in this case R, which determines that the *appearance* of all its offspring shall be dextral. When two)) chromosomes meet they will exert a force equally strong, but in the opposite or sinistral direction.

When two chromosomes meet that differ in type, *viz.* (and), each should theoretically exert an equal and opposite force and the resultant would be zero, *i.e.* a shell and an animal which are bilaterally symmetrical, which in this case is presumably an impossible condition. Practically, the probability would be that in half of these cases one force, and in the other half the other force, would be effectively the stronger and this has been expressed by saying that half the heterozygous nuclei will give an appearance-determiner RL, and half LR, thus:

((	()	)(	))
makes	makes	makes	makes
R	RL	LR	L

Fig. 1 gives two pedigree tables showing the behaviour of these four types, the nuclear composition of each individual being shown above while the appearance-determiner for the next generation is shown below. From this it will be seen that each of the four types of nuclear composition can make only the particular appearance-determiner appropriate to that type. For convenience therefore the genotypical constitutions of individuals will be referred to below by their appearance-determiners only, while the phenotypical results are referred to as dextral and sinistral. It will be seen that the parents in pedigrees (*a*) and (*b*) are both shown as sinistral in appearance and heterozygous in composition and in both cases the results in the *second* generation are identical. The difference is found in the *first* generation: in (*a*) the snails, derived from an LR parent, are all *sinistral* in appearance; in (*b*) derived from an RL parent, they are all *dextral*. Had the parents in both cases been of the same composition but *dextral* in appearance, the results in the 1st and 2nd generations would still have been the same. Hence the constitution of any particular isolated single cannot be fully determined until the broods of the 2nd generation have been obtained.

This consideration led us to the examination of groups of broods derived from a common grandparent, *i.e.* first-cousin groups. In our preliminary paper we classified these groups under five headings:

α	β	γ	δ	ε
All broods dextral	3 broods dextral to 1 sinistral	1 brood dextral to 1 sinistral	1 brood dextral to 3 sinistral	All broods sinistral

It is clear from the pedigrees in Fig. 1 that when isolated singles alone are used only three types of first-cousin groups are possible:

An R parent gives in the 2nd generation an α group.

An L parent gives in the 2nd generation an ϵ group.

A heterozygous parent, whether RL or LR, gives in the 2nd generation a γ group.

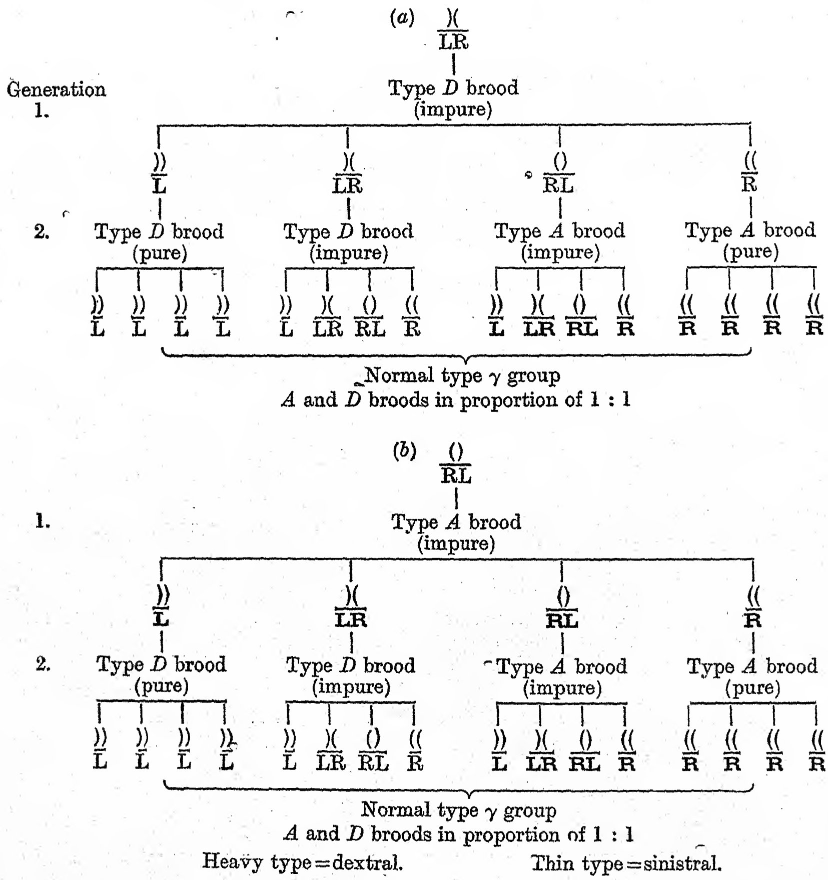

Fig. 1. Pedigree table to show "normal" inheritance through isolated singles only. (*a*) Family derived from a sinistral heterozygote of LR type. (*b*) Family derived from a sinistral heterozygote of RL type.

β and δ groups obviously can only arise from the cross homozygote $\times$ heterozygote and their existence is dependent on the supposition that both types of heterozygotes will be present among the offspring. For

instance, if a homozygote R is crossed with a heterozygote RL or LR the 1st generation will be made up in the following proportions:

R	RL	LR
2	1	1

and if the individuals of this brood are self-fertilized the 2nd generation will appear as a type β group. Similarly if a homozygote L is crossed with either heterozygote, the 1st generation will be made up in the proportions:

RL	LR	L
1	1	2

which appears in the 2nd generation as a type δ group.

It follows from this that if the parent was a single there are two kinds of *A* broods, *viz.* those which carried on will give α groups and those which will give γ groups. Whereas if the parents were a pair, three kinds may appear which for convenience may be called $A\alpha$, $A\beta$ and $A\gamma$. The same applies naturally to *D* broods; if the parent is a single, $D\gamma$ and $D\epsilon$ are possible, if a pair has been used $D\gamma$, $D\delta$ and $D\epsilon$ may be present. The proportion in which the various types of groups are likely to be found may be easily worked out on simple Mendelian lines.

Suppose that, instead of carrying on the 1st generation brood by means of isolated singles, we proceed by the use of pairs. In an $A\gamma$ or $D\gamma$ brood all four types of snail are present in equal numbers; sixteen crosses (including reciprocals) are therefore possible, which may be tabulated as follows:

Appearance-determiner		First generation *brood* type	Second generation *group* type
1	R × R	*A*	α
2, 3	R × RL	*A*	β
4, 5	R × LR	?	β
6	RL × RL	*A*	γ
7, 8	RL × LR	*B*	γ
9, 10	R × L	*C*	γ
11	LR × LR	*D*	γ
12, 13	L × RL	?	δ
14, 15	L × LR	*D*	δ
16	L × L	*D*	ϵ

In the first column are shown the appearance-determiners of the parental pair; in the second the *first* generation *brood* type; in the third the *second* generation *group* type which would be expected had the 1st generation brood (irrespective of individual appearance) been treated as singles. The results that would follow if the 1st generation brood were treated as pairs may readily be worked out; the only trouble arises in

the mixed broods (*B* and *C*) where, for safety, pairing must in practice be restricted to individuals of like appearance.

It follows from this table that groups of types α and ϵ, and probably β and δ, are of one sort only; γ groups on the other hand may be of two sorts, those derived from a heterozygous pair which will have the composition shown in Fig. 1 and from which in the *third* generation α, γ and ϵ groups may be derived, and those got by pairing homozygotes with opposite determiners in which case the *third* generation will consist of γ groups only.

In crosses 4, 5 and 12, 13 the 1st generation brood type has not been specified. Clearly in these cases there are two possibilities. Either type *C* broods might result from the R or RL parents giving only dextrals while the LR or L parents gave only sinistrals; or the weaker constitution might be overcome by the stronger, in which case R × LR would give an *A* brood and L × RL a *D*. The answer cannot be given definitely until further work has been done with pairs; such evidence as is available is dealt with below (Section 15).

The general hypothesis has been stated above in its simplest form, first by assuming that only one pair of factors is involved and secondly by disregarding the mechanism responsible for the production of broods of types *E* and *F*. Whether the first assumption represents the actual facts or whether future work will confirm the possibility that a two-pair system may be in operation, is immaterial for our present purpose. So far as *E* and *F* broods are concerned, it will be shown in later sections (18 *et seq.*) that, in practice, *when we proceed with isolated singles through a succession of generations* the simple expectation is not fulfilled, but we find instead that in certain cases *A* (*all dextral*) broods may be replaced by type *E* (mostly *sinistral* with a few odd dextrals), and *D* (all *sinistral*) broods by type *F* (mostly *dextral* with a few odd sinistrals). This phenomenon is hereafter referred to as "suppression." The evidence derived from *E* and *F* broods and from the first-cousin groups in which they are found (analysed in detail in Sections 18–28) strongly suggests that *E* broods are really *A* broods in which the all-dextral appearance of the brood has been "suppressed" and *F* broods are really *D* broods in which the all-sinistral appearance has been "suppressed." *E* and *F* broods are thus referred to generally as "suppressed" broods and the first-cousin groups in which such broods occur in an orderly manner are referred to as "suppressed" groups (see Table V). Thus the five types of groups set out above (p. 131) may be found either in a "normal" (Sections 13 and 14) or in a "suppressed" (Sections 24 and 25) form, but the underlying system is the same.

9. SUGGESTED MECHANISMS.

The questions now arise: "On what mechanical basis can a change of the order of total inversion rest?" and "Would such a mechanism give rise to the system implicit in the general hypothesis?"

In considering this matter, four points must be remembered:

(i) The change must be such that it alters *ab initio* the symmetry of development.

(ii) It must be fairly readily brought about.

(iii) It must be of such an order that the specificity of the cell contents is unaffected.

(iv) Since it follows an orderly system of inheritance, it must be resident in the germ cell itself.

Types of inversion that are apparently sporadic have been considered by several authors (Call, 1880; Conklin, 1903) possibly to be due to the effects of pressure on the segmenting egg. This may be, perhaps, a cause of *real* sporadic inversion, but, as I have already suggested above and hope to show in detail in later sections, at least the great majority of those cases of inversion which seem to be anomalous are in fact nothing of the sort in that they occupy a definite place in an orderly system of inheritance. Such cases cannot, therefore, be referred to the *direct* fortuitous effects of external conditions.

The problem of the cause of inversion has been reviewed by Conklin (1903). He points out that the suggestions put forward up to that time do not provide an adequate answer. Following the line of thought behind Crampton's (1894) work he suggests that inversion of symmetry may be produced by an inversion of the polarity of the egg. He has shown that this supposed inversion of polarity is not present in the fully formed ovarian egg and therefore, if it occurs at all, it must be after the eggs are set free. Although he establishes a good case for this hypothesis, he admits that the evidence then at his disposal falls short of actual proof. Such an explanation meets the four points set out above.

Newman (1923) in his study of twinning arrives at a general theory of symmetry-reversal based on the conception that a perfectly bilaterally symmetrical organism is "the resultant of an intimate interplay and cooperation of two systems of primordia which are in focus upon a single median plane" (p. 185) and consequently the basis of asymmetry "seems to be one involving a physiological superiority of one side or the other. In last analysis the difference between the two sides may be reduced to terms of rate of fundamental vital activity, probably measurable in

terms of rate of oxidation" (p. 186). This extremely attractive theory still leaves us, however, the unsolved problem of the basic structure upon which such a difference may depend, a problem upon which the present writer is not in a position to offer any original contribution. All the same it is not without interest to see whether the suggestions put forward by workers in other fields form a possible basis for the system of inheritance here proposed.

The possible analogy between symmetry or asymmetry in living organisms and symmetry or asymmetry in molecular structure or crystal formation must have been present in the minds of all who have considered this subject, and has been expressed by not a few. Newman (p. 177) finds it "extremely attractive and almost unescapable whenever an attempt is made at an ultimate analysis of organic symmetry." The suggestion, however, is one which is fraught with difficulties. Child (1923), in reviewing the subject, rejects the idea in favour of a gradient system.

To attempt a discussion here of the relative merits of these ideas would be out of place, but it is important to note that, so far as the general hypothesis is concerned, either of these possibilities would form an intelligible basis, and the position may be stated as a special case of E. B. Wilson's (1906, p. 424) general conception of the organization of the cell. The primary determining cause of a particular asymmetrical type of development lies in the nucleus, which operates by bringing about specific changes in the cell substance. This process takes place during the development of the germ-cell lineage (consequently time may prove to be an important factor). The differentiations set up by this process form as it were a "framework," more or less firmly fixed in different cases, which determines the type of asymmetry developed by the subsequent operations of the cell.

Conklin (1923) considers that the differentiation determining the symmetry or asymmetry of an individual is to be found in the cytoplasm, and consequently, that the system of inheritance of the sinistral or dextral pattern in Mollusca may be called "maternal inheritance" or "pre-inheritance." As I have shown, however, some of our results do not readily lend themselves to interpretation on a system of simple maternal inheritance and I have, therefore, in the last paragraph, used the wider term "cell substance" in place of the more restricted term cytoplasm. By this I mean to suggest that, although in all probability the cytoplasm is the seat of this "framework," the evidence from *B* broods (Section 12) indicates the possibility that the nature of this "framework" (the appearance-determiner) may in certain cases be reversed *after* the entrance of

the spermatozoon so that the resultant individual does *not* bear the impress of the egg cytoplasm alone.

10. BROOD-TYPES.

It was soon apparent from our experiments that any of the six brood-types might be obtained from parents irrespective of whether they were dextral or sinistral in appearance. The following diagram shows how far this has been realized up to date: the actual figures are not shown; they may be obtained from the pedigree tables.

Brood types		*A*	*B*	*C*	*D*	*E*	*F*	All eggs addled
Pairs	Dextral	+	+	+	+			
	Sinistral	+	+	+	+	+		+
Singles	Dextral	+			+	+	+	+
	Sinistral	+			+	+		+

Apart from the absence of *B* and *C* broods where the parents have been singles, there are five gaps yet to fill. The experiments which are theoretically required to fill them have not yet been made. The gap in the *E* column would presumably be filled by pairing odd dextrals from *E* broods, which would also fill the gap in the last column. The three gaps in the *F* column are due to the fact that, owing to the composition of the original stock, the requisite material is only just beginning to be available. The gaps should be filled by pairing or isolating odd sinistrals from *F* broods and by pairing their dextral sisters. It may be mentioned here that undoubted *F* broods have been recorded by Hargreaves (1919) from wild sinistrals, which is just where the general hypothesis would expect them to occur.

The gaps in the *B* and *C* columns are of a different order. This fact is most strikingly shown by tabulating the actual numbers obtained in each class.

	A	*B*	*C*	*D*	*E*	*F*
Pairs	12	4	4	52	7	—
Singles	123	—	—	353	63	7

The table omits one mixed brood (SP 36, Table I) which, for reasons to be discussed later, is difficult to classify. Beyond this single case, the pedigree tables show that from the composition both of the brood and of the group there is no danger of classing as *E* and *F* broods which ought to be classed as *B* and *C*. From the figures given below it appears that *B* and *C* broods themselves can be separated from each other with equal certainty. Excluding *E* and *F* broods, the figures for all the mixed broods obtained are:

Table	Reference number of parents	Number of young: Dextral	Sinistral	Brood-type
II	DP 656	38	29	*C*
IV	SP (Rad. pair)	147	58	*B*
IV	DP 46	243	83	*B*
IV	DP 47	151	49	*B*
IV	SP 71	118	110	*C*
IV	DP 3551	68	23	*B*
VI	DP 2001 × 2002	63	42	*C*
VI	DP 2022 × 2023	132	183	*C*
(I	SP 36	143	13	?)

The last is the doubtful case in which the parents were subjected to experimental interference.

The special circumstances affecting these ratios and the distribution of these broods in groups must now be considered.

11. Type *C* Broods.

Up to the end of the 1922 season, only one brood that clearly belonged to type *C* had been obtained (SP 71). As soon as it became apparent which crosses were likely to produce broods of this nature, the requisite pairs were set and, early in 1923, two further broods were obtained (DP 2001 × 2002 and DP 2022 × 2023). The fourth brood (DP 656) arose from an accidental pairing.

It seemed probable from our general results that type *C* broods were not really "mixed" broods, *i.e.* broods in which both parents were giving young of both types, therefore the pairs set in 1923, from which broods of this type might be expected, were kept under close observation.

DP 2001 × 2002 (Table VI). In 1922 a number of the young snails from DP 75 were isolated as singles. By the end of that season only three of these had bred, but the result showed fairly clearly that the constitution of the DP 75 brood was $A\gamma$. Therefore, if the snails which had failed to breed as singles were paired, broods of types *B* and *C* might be expected. In March 1923 these pairings were made and some of the individuals of these pairs were re-isolated after pairing had been observed in order to find out how the eggs were deposited by the respective parents. In this particular case the animals were put together in a jam jar on 10th March, 1923. As each individual had been isolated from birth and had failed to breed, the question of previous fertilization does not arise. Pairings were observed a few days after the snails were put together and the two individuals were re-isolated twenty days later on the 30th March.

2002 started laying on the 3rd April, whereas the first eggs seen in 2001 were found on the 10th April. Each capsule of eggs was isolated in

a separate jam jar as soon as it appeared; six capsules were so isolated for 2001, and four for 2002.

It was thus seen that 2001 was producing an all dextral brood while 2002 was producing an all sinistral brood. The parent 2001 was found dead in the second week in May whereas 2002 lived on but ceased laying. Counts of the total broods produced by the two parents showed that 2001 gave 63 dextrals and 2002 gave 42 sinistrals, one of which was abnormal.

DP 2022 × 2023 (Table VI). This pair had also been individually isolated since birth and had failed to breed on self-fertilization during the summer of 1922. On the 10th March, 1923, they were put together in a large jar. No observation of pairing was made in this case and the animals were not separated. By the 23rd April plenty of egg capsules, some of them nearly hatched, were observed. On the 20th June a large brood had hatched, with a preponderance of dextrals. One parent was found to have died quite recently; the other parent was living and there were some recently deposited eggs in the jar. The living parent was immediately transferred to another jar and the unhatched eggs were transferred to a third jar.

On a subsequent count it was found that in the original jar there were:

	Dex.	Sin.
	132	108
There were also two abnormalities, one being completely scalariform, the other being completely flat coiled. As both had died shortly after birth it was impossible to determine whether these were dextral or sinistral; they have therefore been left out		
In the third jar to which the unhatched eggs had been transferred the young were all sinistral	—	23
In the second jar to which the still living parent had been transferred a fresh brood of young soon appeared. These were also all sinistral ...	—	52
Total	132	183

This pair, therefore, was apparently behaving in the same manner as DP 2001 × 2002. In other words, one parent was giving all dextral and the other all sinistral.

Up to the time of the death of the dextral-laying parent the number of young produced by each parent was almost exactly equal—132 dextral to 131 sinistral.

No detailed observations are available in the other two cases (SP 71 and DP 656), but there can now be little doubt that type *C* broods are produced in the manner observed in DP 2001 × 2002. Large divergencies from the 1 : 1 ratio are thus naturally liable to occur as the numbers of each sort will be definitely affected by the relative fecundity and length of life of the two parents. This error should, however, be compensating where a reasonable number of cases are considered.

The four broods of this type so far obtained give the following results:

	Dextral	Sinistral
SP 71	118	110
DP 2001 × 2002	63	42
DP 2022 × 2023	132	183
DP 656	38	29
Total	351	364
Expectation	*357·5*	*357·5*

which show an error towards the sinistrals of 6·5 in 715 or less than 1 per cent.

From these results it may safely be stated that type *C* broods are not the same thing as the ordinary Mendelian equality ratio obtained from the back-cross of the heterozygote to the recessive. On the general hypothesis it seems most likely that *C* broods would result from the cross R × L and its reciprocal. Such a brood must consist entirely of RL and LR individuals. If, as seems likely, these two types are evenly distributed among both the dextral and the sinistral snails the result of making pairs in such a brood would be to give brood types *A*, *B*, *D*, in the proportion of 1 : 2 : 1, *C* broods being absent.

It is hoped to test this during the 1924 breeding season.

It is possible, though on the present evidence less likely, that the crosses R × LR and RL × L and their reciprocals may also give *C* broods. If this were the case the expectation from pairs in an impure strain would be very different.

It will perhaps be convenient to deal here with the special case of SP 36 (Table II).

The individuals of this pair were originally set as singles to breed in the summer of 1921 but in May 1921 they were paired up.

Early in July young snails and eggs were recorded and on the 13th July, in the middle of the laying season and after they had only been together about two months, the parents were killed. On this date the examination of the young revealed the fact that although there were many dextrals as small as the sinistrals, all the larger snails were dextral.

The subsequent results (Table II) show that reciprocal matings probably took place at some time but the possibility that some of the dextrals were produced by self-fertilization prior to the matings is not excluded; further, in my experience, the time elapsing between the two matings (and consequently the time at which each individual commences laying) may be considerable. Thus it is just possible that this represents a *C* brood in which the sinistral throwing parent was killed before it had really got started. However, from the general behaviour of the London

family (Section 27) it is more than likely that it represents an irregular ratio due to the incidence of suppression.

12. TYPE *B* BROODS.

The four broods clearly belonging to this class all occurred in the Radlett family (Table IV) early in the experiment. The Radlett sinistral pair itself gave one. Two more were obtained from dextral pairs drawn from this original *B* brood, and the fourth resulted accidentally from a dextral pair of Miss Garstang's. The first three were obtained before the importance of this type of brood was realized, and the whole of Miss Garstang's brood unfortunately died without issue, so that it is not yet possible from direct evidence based on the separation of the egg-clutches fully to substantiate the position taken up in our preliminary paper, namely that in mixed broods dextrality seems to behave as a simple Mendelian dominant. The indirect evidence, however, seems so strong as to compel us to face this difficult conclusion.

The four broods considered individually and collectively on the 3 : 1 expectation give the following results:

	Result: Dextral	Sinistral
SP (Radlett pair 1st brood)	147	58
Expectation	*153·75*	*51·25*
An error towards the sinistrals of 6·75 in 205, or 3·3 per cent. This error, which is comparatively large, may in part at least be discounted by the fact that the records for this initial brood are not clear and the figures given for the dextrals are possibly a few short		
DP 46	243	83
Expectation	*244·5*	*81·5*
DP 47	151	49
Expectation	*150*	*50*
DP 3551	68	23
Expectation	*68·25*	*22·75*
In these cases where the accuracy of the result is not in doubt the expectation is almost exactly fulfilled: the error in all three cases being ·5 per cent. or less.		
Total	609	213
Expectation	*616·5*	*205·5*

Thus the divergence on all four is less than 1 per cent. in favour of the sinistrals. Such an exact conformity to expectation is too striking to be neglected.

Apart from the evidence of the relative distribution of the two types *B* and *C*, which will be dealt with later (Section 15), the figures can be looked at in another way. Suppose we assume for the moment that there is no actual difference between *B* and *C* broods; that in fact *B* broods are a selection of fortuitous ratios to the making up of which one parent has

contributed the dextrals only and the other the sinistrals. Then in a sample of such "mixed" broods in which the broods might be any size from 2 up to the largest, which is 326, the mathematical probability of getting an *exact* 3 : 1 ratio is 654 to 1 against, and the probability of the occurrence of a ratio so close to this four times in a sample of eight is in the neighbourhood of 10^8 to 1 against. In the face of such probabilities the occurrence of this ratio cannot be regarded as fortuitous. It either indicates that the normal Mendelian 3 : 1 ratio is present or that (on the assumption that no real mixed broods are being produced) the fecundity of the parent throwing the dextral half of the brood may under certain conditions be exactly three times that of the parent throwing the sinistral half.

That the figures do not fall into a single group is further shown by an examination of the total of the eight broods, which shows 960 dextrals to 577 sinistrals. The probability against this being a fortuitous variation from the 1 : 1 ratio is very large indeed, and would be even greater if the 9th brood SP 36 were included, and I am driven to the conclusion that the two separate groups originally presupposed by us do in fact exist.

Two questions now present themselves. What evidence is there for and against the possibility of a mixture being given by each parent? and, if such a mixture is present, how can it be explained in terms of the general hypothesis?

The evidence against a real mixture being present rests on two grounds:

(i) The hypothetical difficulty of explanation in view of the general system of inheritance revealed: a position which is untenable unless strongly supported by experimental fact.

(ii) The complete absence of mixtures revealed by the extensive researches of Mayer (1902) and Crampton (1917) on *Partula*[1]. As is well known, the species examined by these authors are viviparous and *P. otaheitana* is freely amphidromic. The snails dealt with were collected wild and the young when present were dissected out and examined. Both authors found that dextral snails might contain sinistral young and *vice versa*, but in no case did they find young of *both* types in the same snail. This fact looks significant till the actual state of affairs is considered.

First, by the application of the general hypothesis to Crampton's

[1] Since this was written H. E. Crampton (*Science*, LIX. pp. 558–559, 20th June, 1924) has reported that in the examination of *Partula* material from the island of Moorea, five (out of 148 cases where more than two young were present in one brood-pouch) were found in which dextral and sinistral young occurred simultaneously in the same parental brood-pouch. All five cases are reported for *P. suturalis* from one locus.

considerable body of figures representing random samples of different populations an approximate idea can be reached of the likelihood of the requisite crosses occurring in any given population. Since cross-mating between the two phenotypes is practically ruled out, it will be found that in most cases the chances of a *B* brood occurring are quite small.

Secondly, the figures show that the number of young (excluding unhatched eggs) per gravid snail can seldom be more than two and must frequently be only one. Thus the chances of detecting a 3 : 1 mixture are very much reduced.

Thirdly, assuming that the inheritance of coiling in *Partula* follows the same system as that found in other snails, mixed broods of types *E* and *F* must be, and from several of Crampton's groups clearly are, present. For the reasons given above these mixtures also have escaped detection.

On the other side, that real mixtures can exist the general evidence leaves no doubt. Call (1880) demonstrated the presence of mixtures of type *F* in *Campeloma* (*Melantho*). Pelseneer (1920, p. 742) records the fact that similar mixtures have been found in gravid examples of *Clausilia fussiana*. In *Limnaea* mixtures of types *E* and *F* in isolated singles are fairly frequent; the group derived from SS 331 (Table V) forms a striking instance. Adams (1923) attempted to cross a sinistral snail with a dextral. The preliminary attempts at mating were obviously ineffective, but he considers it just possible that a mating may have been ultimately achieved. The egg-capsules were isolated as laid and contained either all dextral or all sinistral young except in the case of two capsules which were mixed containing together 11 dextrals and 11 sinistrals. Nelson (1901) states definitely that both phenotypes were found in the same egg-mass. The figures given by Hargreaves (1919) also show mixtures from single egg-masses.

Further evidence is available from the Radlett pair. In their first season this pair gave an undoubted *B* brood. One of the snails then died and the other was isolated. In the next year this animal gave another brood (Table IV) containing 3 dextrals and 62 sinistrals, which was again followed in the same season by a brood of 58 sinistrals. Disregarding its previous history and subsequent behaviour this second-year brood has the appearance of belonging to type *E*. The analysis of the brood in the next generation casts considerable doubt on this explanation and it seems more than probable that the brood represents the self-fertilization of the remaining LR individual (the RL individual having died at the end of the first season): the three dextrals arising as the result of the delayed action of the sperm introduced by cross-fertilization in the previous season. If

this is so, the second and third broods of this family should, taken together, give a normal γ group, which in fact they do (Section 14):

	Dextral	Sinistral
Snails having determiners:	10	8
Expectation	*9*	*9*

Our first question is thus answered. The general evidence leaves no doubt that in certain cases mixtures may be given by one or both parents, and there are indications that *B* broods are the result of both parents giving a mixture in the proportion of three dextrals to one sinistral. The explanation of this conclusion in terms of the general hypothesis is by no means easy.

Both from theoretical considerations and from the subsequent behaviour of the Radlett family it seems clear that a *B* brood results from the cross RL × LR and its reciprocal. That is, both animals are heterozygous in composition and have weak but opposite appearance-determiners. The production of a true mixed brood from such a cross involves the conclusion that the *final* determination of the asymmetrical appearance of the adult must take place after and not before the entrance of the spermatozoon into the egg. This is not at variance with the general hypothesis or the available evidence. In all cases of self-fertilization and in half the possible crosses (see p. 133) the action of the spermatozoon is merely to confirm the organization of the egg. The results of the R × L cross are equally intelligible either way, and we are left only with the uncertain results of the crosses R × LR and RL × L. The genetical solution of this problem will therefore depend in part at least upon whether *C* broods invariably give γ groups in the next generation or whether *C* broods may be obtained that will give β and δ groups. The real difficulty lies in suggesting how the combined action of the egg and the sperm produces a brood of mixed appearance. It must be assumed either that the determiners cancel out and that the appearance of the brood is determined in the normal Mendelian manner, *i.e.* that the new chromosome composition has a direct, instead of a delayed, action; or that the expressions RL and LR only approximately represent an organization which must be far from simple, and that there are two or more grades of each of these types. The differences between these grades may, for the purpose of argument, be assumed to be small extra "doses" of dextrality or sinistrality, the extra "dose" of dextrality being relatively stronger (other things being equal) than the extra "dose" of sinistrality. In this way a 3 : 1 brood would be obtained in which the new nuclear types would be distributed among the sinistrals in the same proportions

as they are among the dextrals. The crucial test therefore of the two hypotheses lies in the subsequent behaviour of the sinistrals in a *B* brood. In the former case these sinistrals, if carried on as singles, should give an ϵ group as they must, *ex hypothesi*, be homozygous. In the latter case a type γ group should result. The evidence at present available is indeterminate.

13. First-cousin Groups.

It will perhaps be convenient next to consider the general evidence relating to the five types of first-cousin groups that may be obtained when the individuals of any brood are treated as isolated singles. As is to be expected from the genetical constitution of our original stock, the method of proceeding almost entirely by isolated singles and the incidence of suppression, the information regarding groups other than type γ (Section 14) is scanty.

Type α (pure dextral lines). The greater portion of the London family has not yet reached the stage when α groups, normal or suppressed, may be expected. They should appear in the 5th generation from SP 36 (Table II), and the general behaviour of this family leaves little doubt that this expectation will be fulfilled. A very important case, however, will be found in Table III. Here it will be seen that two *A* broods (SS 4511 and SS 4020) were obtained in the 3rd generation from *isolated single sinistral grand-parents* (SS 12 and SS 17) *both of whom gave all sinistral* (*D*) *broods*. Both the *A* broods have "broken through" in a suppressed γ group (Section 25), therefore the probability of their being homogeneous pure dextral broods is very great. Attempts were made to breed from both broods, but unfortunately the whole of SS 4020 and all save four of SS 4511 perished. Three of these bred and an apparent α group resulted. A parallel brood (SS 2169) to this has now been obtained in the 5th generation of the Radlett family (Table VI) from which it is hoped to breed during the next season.

These broods have an added significance in that they provide unquestionable evidence supporting the hypothesis that there are two types of heterozygote.

In the Radlett family, if the second hypothesis regarding the distribution of genetical types in a *B* brood holds good, the chances of an α group appearing in the 3rd generation are 1/16 if the grand-parents were pairs, and 1/4 if the grand-parents were singles. From the way in which the family has been carried on (Table IV) such a group is hardly to be expected. The only possible group (SP 70) is too small to be significant.

α groups were to be expected in the 4th generation from 2/3 of the *A* broods in the DP 45 group. Unfortunately all these broods failed except DS 166 which again is small.

In the 4th and 5th generations from DP 50 (Table VI) the group from DP 179 and possibly that from DS 2014 seem to belong to this type.

A striking example of a *suppressed* α group (SS 331) will be seen in the 5th generation in Table V.

Type ϵ (pure sinistral lines). This type is better represented than the last: the clearest examples are found in the London family 3rd and 4th generations, SP 27 (Table I) and SS 18 (Table III). Several groups in the Radlett family are almost certainly of this nature. In the 4th generation SS 5014, in the 5th generation SS 2058 (Table V). In the 5th generation DS 2028 and DS 2037 (Table VI).

Types β and δ. The accurate determination of these groups is extremely diffcult at the present stage of the experiment. On the one hand, unless the number of broods in a group is large, it is impossible to say for certain that we are not dealing with a rather irregular γ group. On the other, owing to the effects of suppression, groups that appear to be α or ϵ may on further investigation reveal themselves as having had β or δ composition. In fact it seems not improbable that the suppression of the LR individuals in a β group and the RL in a δ group may be the rule rather than the exception.

	A	*D*
DP 45 (Table IV) giving ... ... probably represents a β group. The attempt to prove this by carrying on all seven broods to the next generation unfortunately failed	6	1
DP 50 (Table VI) only contains ... ... (from singles). The subsequent analysis of this family showed clearly that it was not a pure line and, from the behaviour of the three pairs, the chances of its being a γ group are not great	3	—
	9	1
Expectation	*7·5*	*2·5*
The analysis of the DP 50 family suggests, but only on grounds of general probability, that the 4th generation group from DP 5021 (Table VI) should also be included	1	1
	10	2
Expectation	*9*	*3*

Of δ groups there are no normal examples; in both the possible cases the *A* broods have been suppressed and appear as type *E*. The 3rd generation group from DP 48 (Table V), where suppression is apparently not very strong, closely conforms to the δ expectation, but it cannot be definitely stated that it is not a distorted γ group

	Suppressed *A* or Type *E*	*D*
	6	17
Expectation	*5·75*	*17·25*

The 2nd generation of the London family (Tables I and III) almost certainly belongs to type δ, but in this family the incidence of suppression is erratic and it is difficult to give numbers that would have any real value.

14. FIRST-COUSIN GROUPS OF TYPE γ.

Broods from isolated singles of constitutions LR and RL will contain individuals of constitutions L, LR, RL and R in equal numbers: so also will broods from the crosses RL × RL, RL × LR and LR × LR (see Fig. 1). On the other hand, the cross R × L will give RL and LR in equality.

If a number of individuals in any brood so derived are carried on as isolated singles, the resultant first-cousin groups should contain broods of types *A* and *D* in equal numbers. Although the appearance of the groups in all the above cases is the same, there are in fact two classes:

(*a*) Those derived from heterozygous parents paired or single, *i.e.* from broods of types *A*, *B* or *D*.

(*b*) Those from a pair of different homozygotes, *i.e.* from a brood of type *C*.

Undoubted γ groups have been obtained from *A*, *B* and *D* broods but not yet from type *C* unless SP 36 is ultimately found to belong to this brood-type (see argument, Section 27).

The following normal (*i.e.* not suppressed) groups of this type have been obtained:

(i) From an isolated single grand-parent and isolated single parents.

(Table II)

							Brood-types	
2nd gen. SS 192	3rd gen. **69**							
	(703)	(704)	(705)	(706)	(707)	(708)	*A*	*D*
4th gen.	392	**390**	311	**266**	298	316	2	4

(Table VI)

2nd gen. DS 5020	3rd gen. **23**									
	(5123)	(5125)	(5126)	(5128)	(5132)	(5134)	(5135)	(5136)		
4th gen.	64	**148**	6	**51**	29	**2**	**2**	**112**	5	3
									7	7
								Expectation	7	7

(ii) From paired grand-parents and isolated single parents.

(Table IV)

Radlett pair — 1st gen. **147** and 58

	(53)	(54)	(55)	(58)	(61)	(62)	(64)	(66)	(49)	*A*	*D*
2nd gen.	**92**	**6**	129	78	44	**148**	58	**76**	124	4	5

(Table VI)

2nd gen. DP 75 — 3rd gen. **93**

	(2014)	(2026)	(2028)		
4th gen.	**143**	21	41	1	2

(Table IV)

1st gen. SP 67 — 2nd gen. 15

	(263)	(264)	(3511)	(3512)	(3513)	(3514)	(3515)	(3516)		
3rd gen.	**110**	57	**67**	**109**	**99**	**32**	**238**	71	6	2
									11	9
								Expectation	*10*	*10*
								Total for (i) and (ii)	18	16
								Expectation	*17*	*17*

The analysis can be taken a stage further. In a brood which must hypothetically include all four types of individuals R, RL, LR and L in equal numbers, it is possible by an examination of the behaviour of any pairs set to estimate how the individuals in each pair would have behaved if treated as isolated singles. The accuracy of the analysis in this further stage cannot, of course, be so great, but the errors introduced are of a compensating character (see pp. 133–4) and therefore the results may at least be regarded as instructive.

If the general behaviour of the whole 1st generation (all three broods) from the Radlett pair is analysed, we should expect on the general hypothesis a type γ group to result.

(Whichever hypothesis is applied to the distribution of nuclear material in a *B* brood the general behaviour of the whole group taken together must be the same.)

(Table IV)

Radlett pair: 1st gen., 1st brood

Pairs

	(45)	(46)	(47)	(48)	(50)	(56)	(59)	(60)	A	D
2nd gen. Brood-types	*A A*	*A D*	*A D*	*D D*	*A A*	*D D*	*D D*	*D D*	6	10
Singles as above									4	5

Radlett pair: 2nd and 3rd broods surviving parent (? self-fertilized)

Pairs

	(67)	(70)	(71)	(129)	(130)	A	D
2nd gen. Brood-types	*D D*	*A A*	*A D*	*D D*	*D D*	3	7

Singles

	(72)	(73)	(80)	(122)	(123)	(125)	(127)	(128)	(5001)	A	D
2nd gen. Brood-types	(*E*)	*A*	*A*	*A*	*A*	*A*	*A*	*A*	*D*	7	1
										20	23
Expectation										*21·5*	*21·5*

The presence of a single suppressed brood (*E*) is difficult to understand. It seems obvious from its appearance that it is a suppressed *A*, but I have not included it in the figures.

Another group can be analysed in the same way.

(Table VI)

2nd gen. DP 75 — 3rd gen. **93** (showing pairs only)

	(2019 × 2036)	(2001 × 2002)	(2004 × 2005)	(2011 × 2012)	(2022 × 2023)	(2025 × 2032)	(2033 × 2034)	A	D
4th gen. Brood-types	*A A*	*A D*	*D D*	*D D*	*A D*	*A A*	*A A*	8	6
Singles as above								1	2
Individuals 2006 and 2030 gave								—	2

(2006 was twice paired without apparent result and subsequently gave a small brood probably on self-fertilization.

2030 was paired with a *sinistral*, but it is extremely unlikely that any cross-fertilization took place.)

	A	D
Total	9	10
Expectation	*9·5*	*9·5*

There are two other broods which must, on the general hypothesis, represent γ groups.

(Table VI)

2nd gen.		3rd gen.		
DS 181		**75** (2037)	*A*	*D*
	4th gen.	65	—	1

(Table IV)

1st gen.		2nd gen.		
SS 127		**57** (3551)		
	3rd gen. Brood-types	*A* *D*	1	1
			1	2

A further γ group was obtained from SP 36:

(Table II)

1st gen. SP 36 — 2nd gen. **149 and 13**

The dextrals gave:

	(4108)	(279)	(288)	(289)	(290)	(293)	(294)	(297)	(298)	(300)	(301)	(302)	*A*	*D*
3rd gen.	25	**214**	**66**	**102**	**189**	**18**	101	88	20	**119**	77	**5**	7	5

The sinistrals gave:

	(191)	(192)	(193)	(275)	(4102)	(4103)	*A*	*D*
3rd gen.	**67**	**69**	24	15	88	**58**	3	3
							10	8
						Expectation	*9*	*9*

In this same family five dextral pairs were also successful.

	(160)	(286)	(287)	(4105)	(4106)
3rd gen.	13	**151**	**68**	**3**	23

Taking the broods on their face value this would give six *A* and four *D*, but the brood produced by 4105 is so small that it cannot be regarded as likely that both parents contributed, or that mating took place. The two sinistral broods are also not large so it seems better to disregard this group.

A general total, therefore, of all the groups shows:

	A	*D*
	53	52
Expectation	*52·5*	*52·5*

The number of broods involved is sufficiently great to make this result significant.

15. PROPORTIONATE OCCURRENCE OF BROOD-TYPES *A*, *B*, *C* AND *D* AMONG PAIRS IN AN IMPURE STRAIN.

In Section 8 we considered the hypothetical results of making up pairs in a brood containing all four types R, RL, LR and L in equal numbers, it being left undetermined whether the crosses R × LR and RL × L resulted in *C* broods or *A* and *D* respectively. Both the theoretical considerations advanced in Section 12 and the actual figures make the latter result the more likely.

	A	*B*	*C*	*D*
In the first case the expectation in 16 broods would be	4	2	6	4
In the second case	6	2	2	6

For the purpose of calculating expectations it will be assumed that the second case represents the facts.

The next problem is the distribution of the four types in a *B* brood. As was shown at the end of Section 12 there are two possible hypotheses. The distribution would be:

		R	RL	LR	L
In the first case:					
	Dextrals	1	1	1	—
	Sinistrals	—	—	—	1
In the second case:					
	Dextrals	3	3	3	3
	Sinistrals	1	1	1	1

Again, on general considerations, the second hypothesis seems the more likely.

In this respect the results of *pairings* made from the Radlett pair's first brood (Table IV) may be considered.

On the *first* hypothesis:

		A	*B*	*C*	*D*
Dextrals:	Results	2	2	—	3
	Expectation	*4·7*	*1·5*	—	*·8*
Sinistrals:	Results	—	—	—	1
	Expectation	—	—	—	*All*

On the *second* hypothesis:

(Dextrals and sinistrals have the same expectation.)

	A	*B*	*C*	*D*
Results	2	2	—	4
Expectation	*3*	*1*	*1*	*3*

If we consider the results from *all* the first brood snails whether *paired or single* on the same method as in Section 14, we find snails with:

On the *first* hypothesis:

		Dextral determiners	Sinistral determiners
Dextrals	Results	10	13
	Expectation	*15·3*	*7·6*
Sinistrals	Results	—	3
	Expectation	—	*All*

On the *second* hypothesis:

		Dextral determiners	Sinistral determiners
Dextrals and sinistrals together:	Results	10	16
	Expectation	*13*	*13*

Further, if the A broods are carried on to the next generation, the first-cousin groups expected are the same on both hypotheses (see p. 133):

α	β	γ
1	4	1

and two probable β groups in fact resulted, DP 45 and DP 50.

The D broods on the first hypothesis can only arise from the cross LR $\times$ LR and γ groups alone could result. If this is so, the subsequent behaviour of DP 48 (Table V) is rather more difficult to understand, as it shows some indications of being the δ group expected on the second hypothesis. Several of the individual broods in this group are, however, too small for any reliance to be placed on their appearance.

If for the moment we neglect the pairs made from the Radlett pair's first brood as being doubtful, and compare the results obtained from making pairs in broods which must hypothetically be $A\gamma$ or $D\gamma$, we get the following results:

	A	*B*	*C*	*D*
Radlett pair, 2nd brood 2nd generation (Table IV)	1	—	1	3
DP 75 4th generation (Table VI)	3	—	2	2
SS 127 3rd generation (Table IV)	—	1	—	—
	4	1	3	5
Expectation	*5·5*	*1·8*	*1·8*	*5·5*
If we accept the second hypothesis the results of the Radlett 1st brood may be included and the totals are	6	3	3	9
Expectation	*7·9*	*2·6*	*2·6*	*7·9*
If C broods resulted from the cross R $\times$ LR and RL $\times$ L, the expectation would be	*5·25*	*2·6*	*7·9*	*5·25*

The figures available are small, but the results are suggestive, and in no case has a brood of type B or C occurred where its presence was not to be expected.

The 2nd generation pairs from SP 36 (Table II) have not been included in the above figures for two reasons. First, it is not yet clear

(Section 27) that the expectation is the same in this case. Secondly, the number of snails per brood is unsatisfactorily small and it is just possible that pairing has not in all cases been effective.

The type *C* brood in the 4th generation from SS 4103 (Table II) has also been excluded as it occurs in a γ group where the sinistral appearance is partially suppressed and the expectation from pairs in such a group is as yet unknown.

If it is ultimately shown that these broods may legitimately be included here, the agreement between fact and expectation would be even closer:

	A	*B*	*C*	*D*
	9	3	4	11
Expectation	*10·1*	*3·4*	*3·4*	*10·1*

16. GENERAL ANALYSIS OF THE RADLETT FAMILY. (Tables IV and VI.)

It has been shown in the preceding sections:

(i) That the original parents of this family must have been RL and LR heterozygotes respectively.

(ii) That at the end of their first season the RL individual died and the LR snail gave further broods mainly by self-fertilization.

(iii) That the 2nd generation, whether considered as two groups or one, gives the expected type γ group.

(iv) That the 2nd generation broods obtained from pairs agree with the most probable expectation.

(v) That in the 3rd generation the five groups obtained from 1st generation pairs and the three obtained from singles (barring the incidence of suppression (DP 48) which will be considered later) are also such as might be expected on the general hypothesis.

Of these groups three did not reach a 4th generation and consequently are not available for further breeding. It is therefore not clear whether the sinistral pair 70 were both of constitution R or whether one was R while the other was RL. SS 122 and SS 127 must both have been RL; in the first case suppression has become operative while in the second case this apparently is not so. The erratic incidence of suppression in this family reveals itself in the single *E* brood from SS 72 which seems to be a suppressed RL.

It should be pointed out that the failure to carry on such important broods as DP 46, DP 47, SP 71, etc., must be attributed to a variety

of accidental causes and not to an absence of endeavour. Extensive attempts were made to carry to a 4th generation the groups derived from DP 45 and SS 122 which, except for two broods, entirely failed; so that the only strains still available are those derived from SP 67 (Table IV), DP 50 (Table VI) and DP 48 (Table V).

The DP 48 groups which show regular suppression throughout will be considered in detail in later sections.

SP 67 (Table IV). This pair gave only 15 sinistrals and it seems unlikely that effective pairing took place. (An analogous case kept under close observation may be quoted here; a dextral (2006, Table VI) was paired with another (2007) in March, 1923. Matings were observed but no broods resulted. 2006 was then put with a third dextral which had failed in a similar manner. Between this new pair no matings were observed. Towards the end of July, however, 2006 produced seven sinistrals almost certainly from self-fertilization.)

The 3rd generation group in this case does not help us. It is obviously a γ group and might have resulted from an LR single or the cross LR × LR, both of which are possible under the circumstances. Attempts were made to carry all eight broods to a 4th generation, but in the majority of cases this was not successful. The expectation would be that half the broods would give γ or suppressed γ groups, the other half giving α or ϵ. So far as the figures go this is carried out. The suppressed γ group from SS 263 is considered below (Section 25).

DP 50 (Table VI). It has been shown that, although the 3rd generation broods in this group are all type A, the result in the 4th generation leaves little doubt that it must be a β group in which a sinistral brood has not appeared. All six broods have been carried on. From the pairs: DP 75 gives a clear γ group (Section 14) from the cross RL × RL, and the groups of the 5th generation substantiate this: the expected γ group, as is reasonable under the circumstances, appearing in the suppressed form. DP 179 an α group (R × R) and DP 5021 a γ or more probably β (Section 13). From the singles: DS 181 and DS 5020 are clearly γ groups from RL parents. DS 5019 cannot be disposed of so easily. It has the general appearance of a suppressed γ group and has been dealt with as such in Section 25. The presence of an apparent E brood in this place is very difficult to understand, an F brood would be possible. The chances of this being a mistake do not seem to be great and we must therefore accept it as something which may be elucidated later.

Thus considered through five generations, this family seems to afford a clear illustration of a system of inheritance conformable with the general hypothesis.

17. SUMMARY OF EVIDENCE RELATING DIRECTLY TO THE GENERAL HYPOTHESIS.

The general hypothesis is briefly set out in Section 7, and it is assumed there that the final asymmetry of an individual is determined by the *combined* action of the chromosomes involved, which action has a *delayed* effect. This involves a departure from simple dominance, and the presence of two types of heterozygote. In Section 8 a symbolical notation is suggested whereby the general hypothesis may be expressed, and the general results to be expected from the system are worked out.

The examination of our results shows that:

(i) Broods of all six types may be obtained both from dextral and from sinistral pairs.

(ii) Broods of types *A*, *D*, *E* and *F* may be obtained from dextral or sinistral singles.

(iii) Mixed broods of types *B* and *C* are only obtained from pairs and are readily distinguished both from mixed broods of types *E* and *F* and from each other.

(iv) Type *C* broods are produced by one parent laying only dextral young and the other only sinistral. The variations from the expected 1 : 1 ratio may therefore be large but they should be *compensating*, which is shown to be the case. These broods probably arise from the cross of the pure types R and L.

(v) Type *B* broods conform exactly to the 3 : 1 expectation. There is no direct evidence yet that each parent produces a 3 : 1 ratio, but the indirect evidence is not without weight. There can be little doubt that this type is a real mixture and not the same as type *C*. It seems clear that such a brood results from the cross RL × LR and its reciprocal.

(vi) First-cousin groups of types α, γ and ϵ, expected by the general hypothesis apparently occur where they might reasonably be expected. Incidentally the examination of these groups provides clear evidence of the presence of two types of heterozygote. The presence of groups of types β and δ has not yet been clearly demonstrated: this aspect of the problem is complicated by the phenomenon of suppression.

(vii) The proportionate occurrence of types *A*, *B*, *C* and *D* among pairs in an impure strain, although the figures available are not large, shows a reasonably close agreement with the hypothetical expectation; and in no case has a brood of type *B* or *C* been found in a place where it was not expected.

(viii) The general analysis of the whole Radlett family through five

generations indicates clearly that the inheritance of inversion is following either the system implicit in the general hypothesis, or some other system which implies a very similar expectation.

18. "Suppressed" Inheritance.

It has been shown above that in following up families by means of isolated (self-fertilized) singles, the regular appearance of broods of types A and D necessitated by the general hypothesis does not in fact *always* take place. In a first-cousin group derived from a heterozygous grand-parent two different conditions arise. On the one hand, where the predominant stock is *dextral* we find, not the expected A and D broods in equality (*i.e.* a normal type γ group), but A broods with, here and there, a brood of type F. On the other hand, when the predominant stock is *sinistral* we find D broods with a few broods of type E.

I have suggested that these broods of types E and F should be regarded as "suppressed" broods and the experiments set during the summer of 1923 to test this suggestion appear to have given a very definite answer in its favour (notably in the 4th and 5th generation broods derived from DP 48 (Table V)). If this is so we then find ourselves again, as the general hypothesis predicts, in the presence of a type γ first-cousin group.

In one case we found:

A broods and suppressed D broods (or type F).

In the other:

suppressed A broods (or type E) and D broods.

The former condition has not yet been explored by us as, although its occurrence was predicted, the animals originally used by Boycott were of a genetical composition such that γ groups of the A–F type were not to be expected in the early results and have not been obtained in any working quantity till this last breeding season (for example see Table II, 4th generation group from SS 4103).

It seems possible that as we proceed on our system of in-breeding by means of self-fertilization that these "suppressed" γ groups of the A–F and D–E types may become the rule and it is hoped that in future breeding it may be possible to follow up this line and thus compare the occurrence and behaviour of type F broods with that of type E.

As far as can be seen at present the two conditions would seem to be identical, as the general hypothesis suggests. The latter condition, where the A broods have been "suppressed" and appear as type E, has been explored to a considerable extent.

The London family (Tables I and III) provides much information but the clearest results have been obtained from DP 48 (Table V), several of the groups in this family being a generation in advance of the main experiment.

Apart from the evidence afforded by the predicable regularity with which broods of type *E* occur (Sections 25–27), there is further evidence of something abnormal happening which tends to support the special hypothesis of suppression. Such evidence can be, for convenience, examined under four headings:

(*a*) The relative size (*i.e.* number of young) of the brood.

(*b*) The occurrence of addled eggs.

(*c*) The occurrence of abnormally coiled shells.

(*d*) The fecundity of the odd dextrals.

It is obvious that evidence derived from sources like these must be treated with the utmost caution. External factors, such as range of temperature, degree and type of illumination, generally hard conditions of life, are difficult to control or allow for; particularly as their effect on the results may be direct, or indirect, so as to cause a general weakening in the strain.

19. RELATIVE BROOD SIZES.

Our experiments, conducted as they have been by several workers under different conditions of lighting and temperature, have indicated a considerable variability in the size of the broods. Though no definite experiments have been carried out by us so far to test the relation of apparent fecundity to external conditions there is, as might be expected from the results of other workers, some evidence that the fecundity of an individual may be affected one way or the other by its environment.

This evidence is derived from two sources. First, the number of individuals set as parents which fail to reach maturity or fail to breed, although mature. Secondly, the average size of a group of broods more or less similarly treated.

In this respect SP 36 (Table II), inasmuch as it has been extensively carried on and differentially treated, provides some interesting data.

Twelve of the 3rd generation broods were carried on and gave, in the 4th generation twelve first-cousin groups, 177 of the 3rd generation snails were used as parents, 86 or about 50 per cent. of these were taken from six of the 3rd generation broods; while 91 were taken from the other six. The former batch were among 150 animals particularly set

under optimum conditions (see below), while the latter were subjected to conditions only slightly better than the average for the experiment. All were set as isolated singles except six snails among the former batch which were set as three pairs.

First the number of snails that failed to breed in the two batches respectively may be considered. For this purpose it is better to disregard the three pairs, as although all three gave broods it cannot be definitely stated that both parents were fertile.

	1st batch	2nd batch
Total	80	91
Failed	7	33
Recorded as having given addled eggs	1	3
Percentage of failures	10	39·6

The difference between the two batches is not insignificant.

Secondly we may consider the relative fecundity of the two batches of parents. For this purpose I have, for obvious reasons, included the pairs and assumed, which is very probable, that both parents contributed to the brood.

In order to eliminate as far as possible the chance that the broods in the first batch might have inherited a higher fecundity than those in the second, I have taken the average of the twelve 3rd generation broods from which these 4th generation groups were derived; the actual figures can be seen in Table II.

	Six broods from which 1st batch was taken	Six broods from which 2nd batch was taken
Average size per brood	88·5	102·3

The difference is hardly significant, but such as it is, it is in favour of the second batch.

Disregarding those that failed to breed, the averages of the 4th generation broods are as follows:

	Broods derived from 1st batch parents	Broods derived from 2nd batch parents
Number of broods	75	55
Number of parents involved ...	78	55
Total young produced	15,402	5,097
Average number of young produced by each fertile parent ...	197·5	92·7

or the average fecundity of the parents specially treated was more than twice as great as the average fecundity of those not so treated. If the failures are included the difference is of course even more marked:

	Broods derived from 1st batch parents	Broods derived from 2nd batch parents
Number of parents involved ...	86	91
Average per parent	179·1	56

This method perhaps does not give due weight to small groups of high average fecundity; to cover this I have taken the average for each group, then again averaged these figures. The results are the same.

	Broods derived from 1st batch parents	Broods derived from 2nd batch parents
Including only fertile parents ...	215·8	115
Including fertile and infertile ...	189·3	58·7

As the 3rd generation broods were quite indiscriminately divided between the two batches, and as the 4th generation groups in both batches contain all four types of broods, *A*, *D*, *E* and *F*, these figures must be regarded as significant.

So far as the difference between the two generations is concerned the comparable figures are:

	1st batch	2nd batch
Average 3rd generation broods	88·5	102·3
Average 4th generation broods	197·5	92·7

The difference between the generations of the second batch, so far as it may be considered significant, may be accounted for by the fact that in the 3rd generation no suppressed broods were present while in the 4th generation they were. The difference between the figures for the first batch is very striking.

From this we pass to the consideration of the relative size of the four brood-types, *A*, *D*, *E* and *F*,

(i) when derived from parents placed under similar conditions;

(ii) generally throughout the experiment.

(i) About 150 individuals were set by Boycott in 1923 under precisely similar conditions which, as far as could be determined, were likely to be optimum conditions for breeding. These individuals were drawn partly from the London family and partly from the Radlett family. The results were extremely satisfactory and the number of failures to breed was relatively low. Out of some 150, 21 failed to breed, 100 broods were obtained of types *A* and *D*, 29 of *E* and *F*, and it seemed clear from the results that the broods of types *E* and *F* were definitely smaller than those of types *A* and *D*. In Fig. 2 the broods have been arranged as a frequency polygon. They were divided into size groups, all broods with from 1 to 50 individuals being in the first group and those having 51 to 100 in the second group, and so on. These groups are shown along the abscissa; the percentage of occurrence of each group is shown along the ordinate. It will be seen that all *E* and *F* broods, with the

exception of two were under 200; on the other hand, the *A* and *D* broods describe a normal probability curve about a mean around 250. The regularity of this curve, however, is broken by the large number of broods of types *A* and *D* (mainly *D*) which were under 50 in size. When the various groups of broods are considered individually there is a shortage, on our expectation, of *E* and *F* broods (Section 25). The *A* and *D* curve

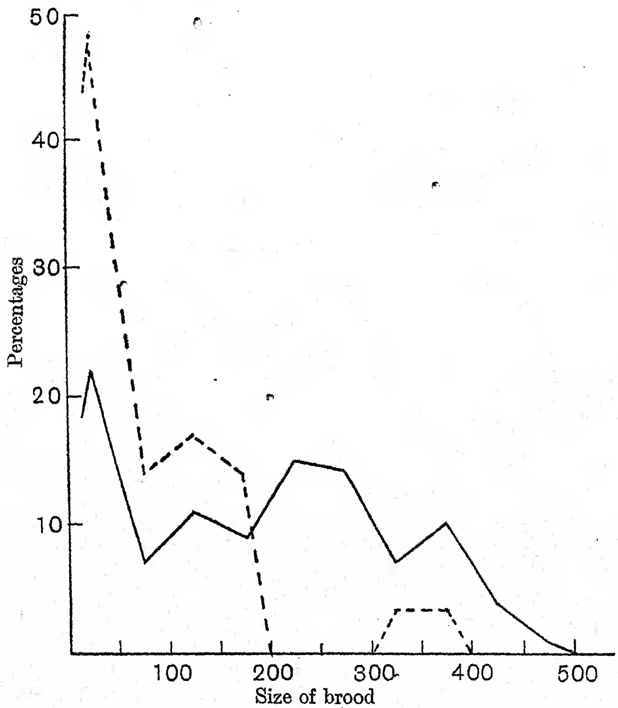

FIG. 2. Showing the relative frequency of brood-sizes as between *unsuppressed* broods of types *A* and *D* (continuous curve) and *suppressed* broods of types *E* and *F* (dotted curve) among the 129 broods ($A+D=100$, $E+F=29$) bred from isolated singles under similar conditions. (See text.)

clearly indicates where some of this shortage is to be looked for. It is, of course, obvious that in many of the broods under 50 the chances of an odd dextral occurring (thus making the brood an *E* instead of a *D* brood) are very much reduced.

One fact which this series of broods seems to have established is that the closest possible inbreeding through three generations has not reduced the general fecundity of the stock. This has also been demonstrated by the work of Colton (1918) who has carried a line of *L. columella* (Say) through 31 self-fertilized generations.

The general problems concerning fecundity will, it is hoped, be considered separately.

(ii) The smaller size of the suppressed broods or the lower fecundity of the parents giving suppressed broods may be demonstrated further.

Dividing all broods from isolated singles into size groups, again with an interval of 50 as in Fig. 2, it will be seen that there is a continuous distribution of broods throughout all the size groups up to a certain point. Above this point one or two abnormally large broods occur that are disconnected from the main series.

In Fig. 3 all broods (from singles) of types *A*, *D*, *E* and *F* have been collected together to show what may be called the range of distribution of the different types, from the smallest to the largest brood obtained of each type.

The number of broods that can be included for this purpose is, for

$$\begin{array}{cccc} A & D & E & F \\ 123 & 353 & \multicolumn{2}{c}{\underbrace{63 \quad 7}_{70}} \end{array}$$

As for the purposes of this argument the *E* and *F* broods are an expression of the same phenomenon, suppression, they have been shown together. The *A* and *D* broods, however, have been kept separate as the figures appear to show an interesting difference between the two types; the *A* broods on the average are larger than the *D* broods.

It will be seen that the *E* and *F* broods are poorly represented which might reasonably account for their more limited range. Against this must be set the fact that 41·4 per cent. of the *E* and *F* broods were among the 150 broods treated to optimum conditions, while only 21 per cent. of the *A* and *D* broods were so treated.

In the *A* broods there is a continuous distribution ranging from 1–422: above this point there is only one brood which gave 792.

In the *D* broods there are no abnormally large broods but a continuous distribution from 1–417, with one at 486.

In the *E* and *F* broods the continuous distribution or normal range ends at 225, there being two broods above this: an *E* brood at 355, and an *F* at 341.

The largest broods in types *A*, *E* and *F* and most of the larger broods at the upper end of the normal range in all four types occur in the 4th generation groups from SP 36.

It will be seen from Fig. 3 that the *E* and *F* broods are definitely smaller and have a relatively narrower range than the *A* broods. The

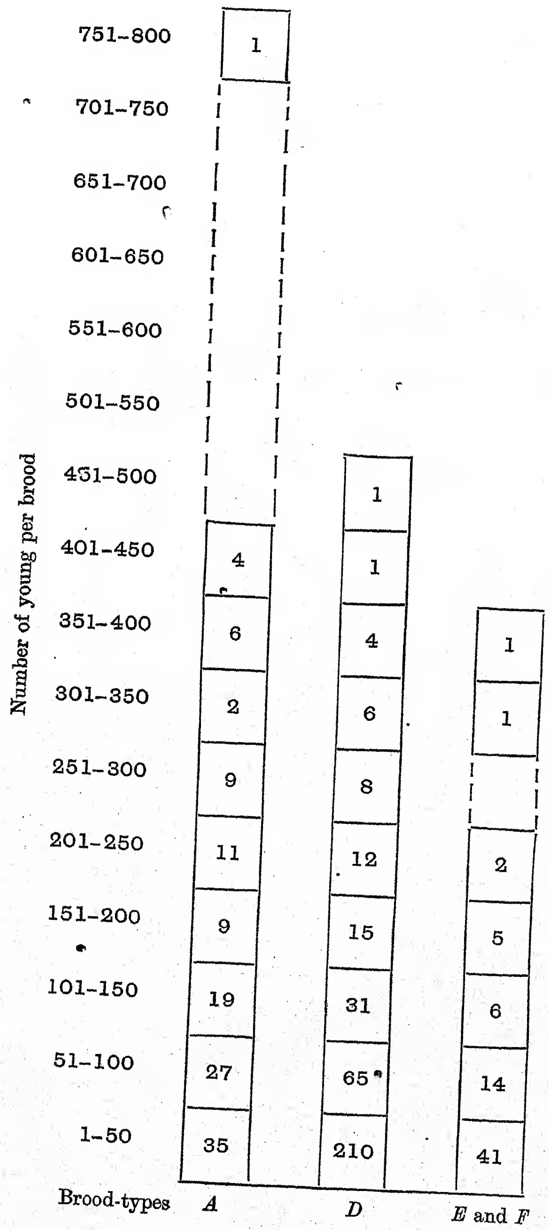

Fig. 3. Showing the comparative distribution of brood-sizes as between broods from isolated singles of types *A*, *D* and *E* and *F* (see Text). The number of broods in each size group is shown within the square.

difference between them and the D broods is not so marked, but allowance must be made for the fact that no fewer than 140 apparent D broods are smaller than 26 and a great many of them occur in suppressed groups. Even without this allowance the average size of the D broods is greater than that of the E and F.

A detailed study of all the suppressed broods including those derived from pairs (*i.e.* a total of 77) reveals another fact. I have proceeded for the last year on the working hypothesis that there are degrees of suppression and that these differences might be used as a rough guide to the genetical composition of the brood. This hypothesis was put to the test particularly with regard to SS 331 (Table V) and the expected result was obtained. Further, the figures at our disposal seem to indicate the presence of some periodic law; but this problem cannot be treated adequately until further data are available.

To illustrate the effect of suppression on fecundity the figures derived from these 77 broods may be grouped in two ways. For the sake of clearness the problem will be stated as it affects D and E broods; the position of A and F broods being hypothetically the same.

First, the broods may be divided into arbitrary groups by the number of "odd" individuals of the opposite type that they contain. Where the brood is of the constitution "suppressed" A, but where suppression is total, the brood will be indistinguishable from type D and must, on our grouping, be placed among the D broods; so that in Fig. 3 the middle column undoubtedly contains, as well as the broods that are normally D, broods that are apparently D through total suppression: so far as fecundity is affected this would probably be a homogeneous group, but it must be remembered that this column almost certainly contains also a number of small broods which would have been classed as E had they been larger. When suppression is not total the brood appears as type E (or F) and will fall into one of the five groups in accordance with whether it contains 1, 2, 3, 4–9, or 10 and over odd dextrals (or odd sinistrals).

Before considering these groups it must be remembered that they are not only arbitrary but very probably heterogeneous. Apart from the errors possibly introduced by human frailty, it is clear that some of the smaller broods might have been very differently grouped had they been bred under optimum conditions.

A brood containing, say, eight young in the proportion of seven sinistrals to one dextral arbitrarily placed in group 1 might in reality belong to groups 2, 3 or 4. If this brood had contained the average number of young found for the SS 331, 5th generation group—namely,

32 (see p. 168)—the chances of its appearing as 28 : 4 or 29 : 3 would at least be equal to the chances of its appearing as 30 : 2 or 31 : 1. The real value of such a brood depends upon the solution of the problem

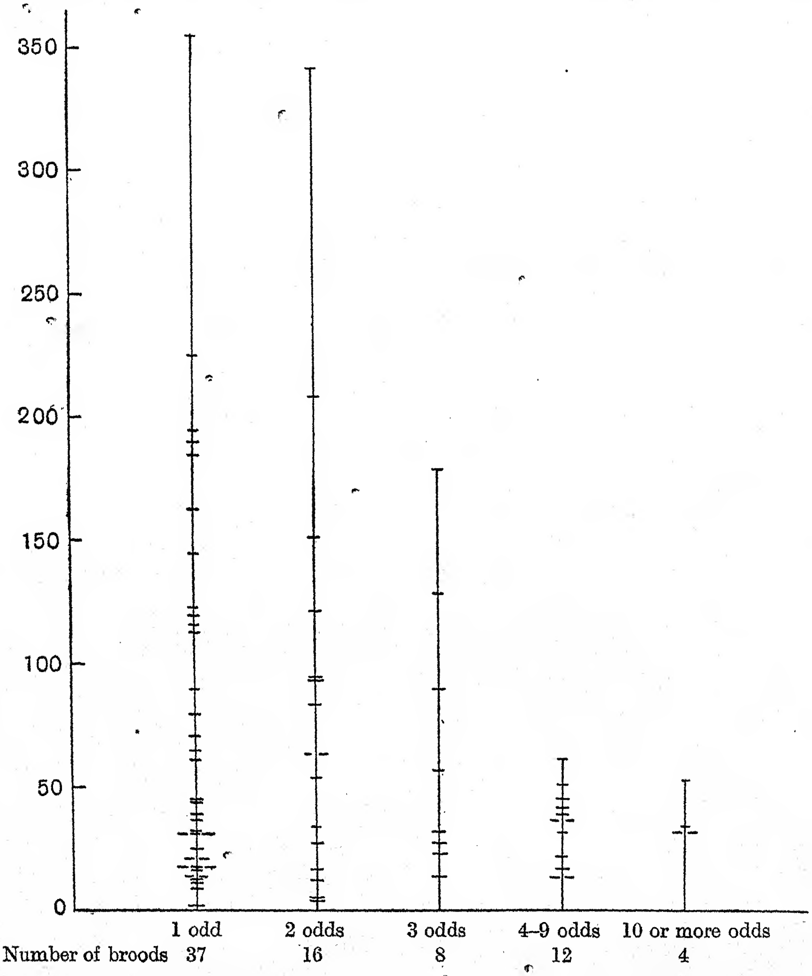

Fig. 4. Showing the distribution of brood-sizes (i.e. number of young per brood) in *E* and *F* broods grouped in accordance with the number of odds (dextral or sinistral) present per brood.

whether the odd dextrals have a systematic or sporadic distribution and whether a time factor is involved.

For this reason, among others, a method based on averages or frequency distribution would tend to obscure rather than reveal the biological facts.

I am fully sensible of the dangers of arguing from the comparative ranges of small samples but a careful scrutiny of the data, coupled with the facts revealed by differential treatment, makes this method quite justifiable (see Fig. 4).

Group 1 (one odd) contains 37 broods and has a range from 2–355 with continuous distribution or normal range ending at 225.

Group 2 (two odds) contains 16 broods and has a normal range from 4–208 with one abnormal brood at 341.

Group 3 (three odds) contains only 8 broods and has a range from 13–179.

Group 4 (from four to nine odds) contains 12 broods. Although the majority of these broods were produced under optimum conditions they are all grouped together within a range from 13–63.

Group 5 (ten or more odds) contains only 4 broods, all of which were produced under optimum conditions but all are closely grouped within a range from 31–53.

It may be contended that the differences in the number of broods contained in each group tends to vitiate the argument, but if for comparison we lump together groups 4 and 5 we get 16 broods giving a range of 50 units; compare this with the 16 broods in group 2 giving a "normal" range of 204 units (that is, disregarding the one big brood in this group) and it becomes clear that the range in the latter case is *four times* that of the former.

Further, in groups 1 and 2 which have *wide* ranges, only 29 per cent. of the broods were treated to optimum conditions, while in groups 3–5 which have *narrow* ranges, 58 per cent. were so treated.

Or, considering the treated broods only: 15 fall into groups 1 and 2 of which 33 per cent. are smaller than 60, and 14 fall into groups 3–5 of which 86 per cent. are smaller than 60.

Secondly, in the same groups the broods may be expressed as a ratio to 1 odd and the range of such ratios considered. In this case for convenience I have only shown the first and last terms of each series (see Fig. 5).

Group 1. Obviously has the same range as in the first case.

Group 2. If the fecundity of the parents of this group was not less than that of group 1 the range should be about halved, which in fact it is.

Group 3. Has a maximum ratio of about 59 : 1 which is just *half* the range expected if the fecundity of the parents was not diminished.

Group 4. In this group the average number of odds per brood is 5·5, so that if the fecundity did not differ between this group and group 3,

the ratios might be expected to have a range of about 30 units, whereas they reach their maximum at less than 9 : 1 or less than *one-third* of this expectation.

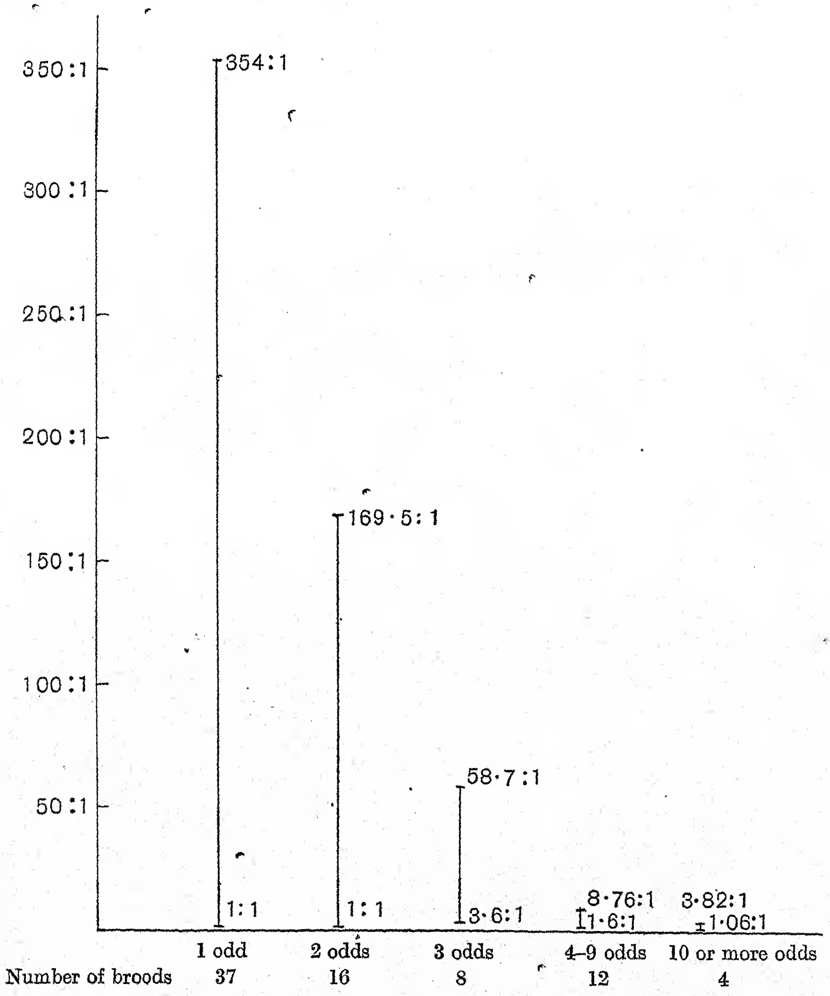

Fig. 5. Showing the range of ratios to 1 odd (dextral or sinistral) in *E* and *F* broods grouped in the same way as in Fig. 4.

Group 5. In this group the average number of odds per brood is 14 (the maximum in any brood so far is 16). If the fecundity of the parents of this group is similar to that of group 4 the range should be about 2/5 of the group 4 range, which in fact it is.

This argument suggests that a less arbitrary grouping could be arrived at which would include all broods derived from isolated singles:

(*a*) Where the broods have a wide size range with many big broods and no odds appearing.

(*b*) Where the broods have a slightly reduced size range with few big broods and one or two odds are present.

(*c*) Where the range is further reduced and three odds are present.

(*d*) Where the range is very limited with no broods above 70 and four or more odds are present.

From the consideration of these figures one fact at least stands out clearly. There is definite evidence of reduced fecundity corresponding with degrees of suppression.

This fact translated into terms of the general hypothesis may be stated as follows:

When the force suppressing the normal operation of the nuclear factors is either sufficiently strong or entirely absent, the determination of the symmetry of cell division is not in doubt and normal fecundity results.

Individual examples of the latter effect will be found in the 3rd generation groups from SS 12 and SS 17 (Table III), where type *A* broods have "broken through" in a suppressed group. In the 4th generation group derived from SS 4103 (Table II) the reverse is illustrated but not so strikingly. The sinistral brood in the 4th generation group derived from DS 300 (Table II) does not, however, lend itself to this interpretation.

As the force of suppression weakens in relation to the force exerted by the nuclear factors, the determination of the symmetry of cell division in individual cases comes more and more into doubt. In its early stages this relative weakening results not only in the production of odd individuals with inverse symmetry but also in the formation of abnormally coiled shells with intorted spires and, in some cases, with completely disconnected whorls (see Section 22 and Plate V), and a reduced number of young. In later stages the broods become increasingly smaller, the number of eggs failing to develop being correspondingly larger, and the ratio of dextrals to sinistrals within a brood approximating to equality.

This last condition is exemplified by the 5th generation group from SS 331 (Table V). The 4th generation brood contained nine sinistrals and four dextrals. From this composition I assumed that it was produced by a parent of constitution "suppressed R" and therefore that, unless the

suppressing force was completely broken through, all broods would show a good percentage of dextrals and consequently a relatively small total number of young per brood.

All 13 individuals were among the 150 animals treated to optimum conditions and are therefore comparable to the figures (given above) for the 4th generation groups from SP 36 (Table II).

Arranged in size groups, with an interval of 10, the 13 broods show the following grouping:

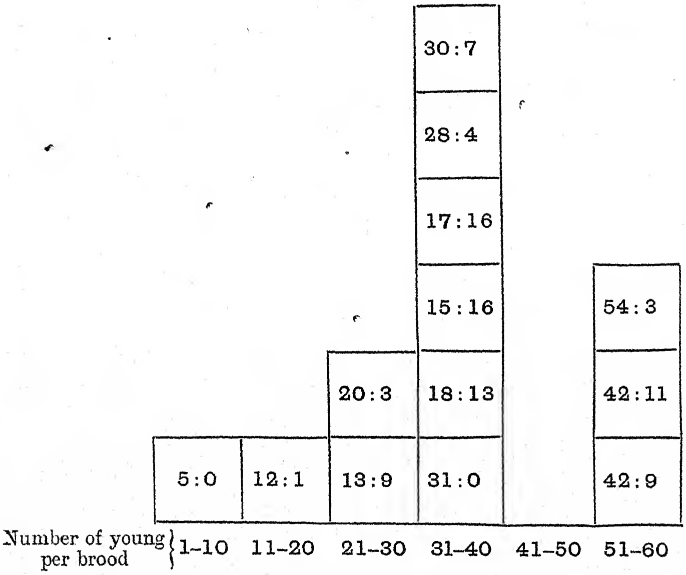

Fig. 6. Showing the distribution, in size groups, of the 13 broods derived from SS 331 (Table V). The numbers within the squares show the proportion of sinistrals to dextrals in each brood.

All 13 broods are closely grouped about the average which is 32·2. The number of broods involved is small but on the other hand their range of distribution is very narrow considering their treatment.

The average fecundity figure of 32·2 is comparable to the average fecundity figures for the six 4th generation groups from SP 36 (Table II). These figures range from the figure for the SS 4102 group—a group in which suppression has a partial effect upon brood size—which is in the neighbourhood of 32×4—to that of the SS 192 group—a group in which suppression is absent—which is in the neighbourhood of 32×10.

Such differences between similar units similarly treated cannot but be significant.

Further, addled eggs were definitely recorded for three of the broods and were probably present in most of them; an abnormal shell is recorded from one brood and in another brood several shells show a slight tendency in this direction.

When it was found that SS 674 was giving a mixed brood, 22 capsules of eggs were individually isolated by Boycott to see how the two types were distributed in the capsules. Of these, however, 17 failed to give any young at all and the remaining five gave a total of only seven.

In case it may be thought that such a result might be attributed to the disturbance of eggs it must be stated that both Boycott and I have followed this method of isolating the egg capsules as laid in several other cases and have found that not only did it have no adverse effect upon the number of young hatching, but that it had a decidedly beneficial effect on their healthiness as shown by a marked decrease in the infantile death-rate.

The general argument from these figures suggests the possibility that real groups exist into which suppressed broods may be properly divided. It is not possible with the data at present at our disposal to declare this as a fact or to say whether there are two such groups or three. As the number of suppressed broods increases during the course of our experiment this ambiguity should be removed, and it should be possible to say whether the small group of broods containing three odds represents a separate condition or whether it is the result of transgressive variation from the two groups on either side.

This problem has a direct bearing on the general hypothesis. A two-group system for suppressed broods is easily understood as resulting from the suppression of RL and R respectively with a relatively stable suppressing force, whereas a system which revealed more than two real groups could be met by one of two explanations in accordance with the distribution and behaviour of the individual broods:

(*a*) It might support the possibility that a heterozygous condition is more prevalent than would be expected if only a single pair of factors were involved.

(*b*) It might strengthen the evidence for an independent variability in the suppressing force apart from its relation to the force exerted by the nuclear factors.

20. Proportionate Occurrence of Odd Dextrals in Broods of Type *E*.

A practical application of this special hypothesis is possible in the groups derived from DP 48 (Table V). In the 3rd generation first-cousin group derived from this pair, 7 broods were obtained from pairs, 23 from singles. In order to avoid the possible errors introduced by the method of pairing it is safer to argue only from the singles. The 23 singles gave:

D broods	*E* broods
17	6

If the constitution of the grand-parents was:

$$\mathrm{L} \times \mathrm{LR}$$

the resulting brood would contain three types in the following proportions:

L	LR	RL
2	1	1

and if the RL were suppressed, as would be reasonable, we should expect on self-fertilizing 24 individuals to obtain:

$$\underbrace{\begin{array}{cc} \mathrm{L} & \mathrm{LR} \\ 12 & 6 \end{array}}_{\substack{18 \\ \text{type } D}} \qquad \begin{array}{c} \mathrm{RL} \\ 6 \\ \\ 6 \\ \text{type } E \end{array}$$

If the constitution of the grand-parents was

LR × LR (or possibly suppressed RL)

the resulting brood would contain four types in equality

L LR RL R

and with suppression operative (which under these circumstances would be less likely), we should expect a first-cousin group containing

12 type *D* : 12 type *E*.

As has been shown elsewhere (Section 15) it is not possible in the present state of our knowledge to say definitely whether one or both of the grand-parents were heterozygous. All that can be said is that an examination of the six *E* broods suggests that they are all derived from suppressed RL parents. Therefore, if the latter condition were present, the expected suppressed R broods have failed to materialize, at least in a recognizable form.

If the *E* broods derived from suppressed RL parents, and such of

the *D* broods as were derived from LR parents are carried on as singles, we should expect to obtain a series of first-cousin groups which would exhibit the suppressed γ formation.

$$\underbrace{\begin{matrix}\text{L} & \qquad & \text{LR}\\ 1 & \qquad & 1\end{matrix}}_{\begin{matrix}2\\ \text{type D}\end{matrix}} \qquad \overset{\text{Suppressed}}{\underbrace{\begin{matrix}\text{RL} & \qquad & \text{R}\\ 1 & \qquad & 1\end{matrix}}_{\begin{matrix}2\\ \text{type } E\end{matrix}}}$$

If a brood derived from a suppressed R parent is again carried on we should expect a suppressed type α group with all broods of type *E*.

(For a detailed discussion of the relative frequency of the types *D* and *E* in this family, see Section 24, "Suppressed α groups," and the first part of Section 25. It is sufficient here to state that expectations and results are in reasonable accord.)

If the special hypothesis is correct, then it is obvious that in a group in which the *E* broods are derived only from RL parents these broods should, on the average, have a relatively large proportion of *sinistrals*. In a group in which the *E* broods may be derived in equal expectation from suppressed RL and suppressed R, the relative quantity of sinistrals should be reduced. While in a group in which all broods should be derived from suppressed R, the nuclear factors operating towards dextrality will be relatively much stronger as compared with the stable, or possibly weakening, force of suppression operating the other way. Consequently the relative quantity of sinistrals should be still further reduced.

The examination of the figures, though it is only a rough test, owing to the difference in value given to the ratios by the effects of external conditions, should make this sufficiently clear.

The six *E* broods in the 3rd generation group, all presumably derived from suppressed RL parents, taken together, give

Sinistral	Dextral
254	8

a ratio to the nearest whole number of 32 : 1.

In the 4th and 5th generations there are several groups derived from single heterozygous grand-parents containing in all 23 type *E* broods. On the general hypothesis half of these *E* broods should be derived from suppressed R and half from suppressed RL parents. Taken together these broods give

Sinistral	Dextral	
765	50	or 15 : 1

There is one group in the 5th generation derived from a suppressed R grand-parent (SS 331). This group contains 11 type *E* broods and 2 apparently type *D*; but as hypothetically this group should be all *E* the sinistrals from the two apparent *D* broods must be included. Taken together the 13 broods give:

Sinistral	Dextral	
327	92	or 4 : 1

or, expressing each brood as a ratio to 1 odd, and taking the average ratio for each of the above three lots, we get the same type of series

32 : 1 22 : 1 9 : 1

In either case the middle term is a reasonable ratio to expect from a mixture of the first and third terms.

The examination can be taken a stage further inasmuch as the mixture in the middle lot can be roughly sorted, from their appearance and relative position, into an R and an RL class. This reveals a shortage in the R class as, at the very most, only nine broods seem to belong here while fourteen belong to the other. The ratios of the two classes, as would be expected from the arbitrary nature of the division, are closely similar to those obtained for the pure classes above.

These figures are sufficiently striking to indicate that the special hypothesis of suppression may have some foundation in fact.

The arraying of evidence that will demonstrate an actual variation in degree of the force of suppression, apart from its relation to the force exerted by the nuclear factors, is, with the figures at our disposal, a much more difficult task. That such a variation in degree does exist seems, from a comparison of the behaviour of the different families and groups in this respect, very probable.

Among the various groups in the DP 48 family, which have the same composition, differences seem to be detectable, but the number of *E* broods from any two groups is insufficient for comparison. There is, however, a much more marked difference between the *E* broods generally and those derived from SP 36 (Table II) in particular. (The figures are compared in detail at the end of Section 25.)

The general argument on this family indicates that six of the groups and possibly all twelve should be either γ or suppressed γ. Table II shows that, on this expectation, there is a very marked shortage of recognizable *E* and *F* broods, and that all these broods, with the exception of one, are relatively very large. The ratio to one odd of all the broods taken

together is 130 : 1. The difference between this and the figures for the DP 48 groups is suggestive. In other words the chances of an odd dextral or an odd sinistral appearing in the SP 36 groups have been very much reduced.

Associated with this greatly increased force of suppression is its disappearance in places where it might be expected to operate. In the groups from 300 and 4103 (Table II) type *D* broods have broken through; in one case in connection with suppressed *D* or type *F* and in the other without such support. In the group from 192 suppression is entirely absent and a normal γ group results; and, what is not insignificant, this group gives the highest average fecundity in the family. A similar absence of suppression occurs in two other branches of the London family.

In spite of the facile explanations that at once suggest themselves, obviously no detailed argument can be based on such scanty evidence, but regarded as information it does provide pointers both towards the special hypothesis and towards methods by which the problem may in future be attacked.

21. OCCURRENCE OF ADDLED EGGS.

During the course of this experiment various workers have occasionally recorded cases where eggs were laid, none of which ultimately developed. In other cases numerous capsules appeared but the resulting brood was relatively small. It was not until the records were all collected together and examined at the end of the last (1923) breeding season that the probability of a connection between the occurrence of addled eggs and the operation of suppression became evident. Consequently our records on this point leave much to be desired; even so the answer they give is fairly definite and provides another link in the chain of evidence.

In all cases where a definite record of addled eggs has been obtained the fact is recorded on the pedigree tables by a + sign; when the record is doubtful in its significance this is preceded by an interrogation mark.

The most dangerous source of error, in the circumstances under which the experiment has been carried out, is the addling of eggs caused by a rise in the water temperature above the critical point. The normal period between laying and hatching is from 2 to 3 weeks, and when the snails are set as singles the large majority of the laying dates fall in July, August and September. Turner has found that the water in his exposed bottles occasionally rose as high as 40° C.; and he attributes most of his records of total or partial addling to this cause although they all fall in groups

where, on the hypothesis of suppression, they would be expected and not in those groups in which suppression is apparently absent.

An experiment conducted by myself for the purpose of detecting, if possible, how mixed broods of types *B* and *C* were distributed between the various capsules, although it partially failed in its main object, throws some light on this problem.

Twelve snails (from a brood of the DP 50 strain where significant addling would not be expected) which had failed to breed in their first season were put together in pairs; when both matings had been observed the snails were individually isolated and each capsule of eggs as laid was again isolated; two pairs failed to give eggs or young.

In three cases the eggs that were found to have failed were counted:

	Young hatched	Addled eggs found
1st case	105	2
2nd case	73	5
3rd case	149	4

In the fourth case the eggs were unfortunately not counted individually, but the records for the capsules show that there were many more failures than in the three cases given above. Out of nine capsules isolated, six contained some eggs that failed. The total brood hatched was 124.

At the same time seven snails (from a brood of the DP 48 strain where suppression is definitely operative) which had also failed to breed in their first season were given free choice of mate and then isolated under precisely similar conditions to those for DP 50. Of these one was accidentally killed; three failed to give eggs or young; three laid eggs: in one case all were addled, in the other two one and ten young hatched respectively, and in both cases there was a large proportion of undeveloped eggs.

Boycott has also in several cases isolated capsules, notably in two suppressed broods from isolated singles that appeared to be giving both types of shell in equal numbers. In the case of the brood from SS 674 (Table V), referred to above (p. 169), 22 capsules were isolated; 17 failed entirely and the remaining five gave a total of only seven young. In the second case 24 capsules of eggs laid by DS 726 (Table IV) only gave eight young.

In another case Boycott made a rough count of the eggs in each capsule deposited by SP 28 (Table I). The total number of eggs was over 300; the subsequent brood contained 162 sinistral and 1 dextral—a loss by addling of about 50 per cent.

These results have made it clear that in future it will be necessary to class records of addling under one of three headings:

(i) Partial.

(ii) Considerable.

(iii) Total.

(i) Partial addling is probably a much more frequent occurrence than our records indicate. It is difficult to detect unless each brood is given individual attention during the hatching period. If only a few eggs per capsule are failing, these eggs become loosened from the jelly mass and may fall to the bottom and disintegrate in a comparatively short time. Turner also informs me that he has found eggs that disintegrate within the capsule during the period occupied by the development of their neighbours, and he is inclined to the view that the appearance of very small broods is presumptive evidence of addling. In some cases this is very probably true; on the other hand, in low fecundity strains I have frequently found newly laid capsules that contained only one to five eggs. As occasional individuals, under close examination, have been found to deposit not more than one or two capsules of this small size, such a presumption may be misleading, and the results may just as readily be regarded as an index of the failure or success of self-fertilization. In any case it seems unlikely that partial addling may be regarded as significant in connection with suppression.

(ii) Where the number of eggs per capsule, or the number of whole capsules, failing in a brood is as great or greater than the number completing development the evidence is clear. Such cases are much less likely to escape notice. Roughly, 25 of the records fall into this class. All are definitely connected with groups where suppression is operative and about 40 per cent. occur in E and F broods.

(iii) Fifteen records of total addling have been obtained that are apparently free from doubt and seven more, the significance of which is questionable. All except one doubtful case occur in suppressed γ groups.

22. OCCURRENCE OF ABNORMALITIES.

The problem involved here is of considerable complexity and the evidence is quite insufficient for quantitative treatment, but, considered as information, it is not without significance. The term abnormality is very wide, but it is used in this case to cover two more or less definite types of variation in the form of the shell. In many species of gastropods individual abnormalities of the shell have been recorded. Pelseneer (1920) has collected together most of these scattered records. The abnormalities with which we are concerned here relate entirely to the

type of *spiral* exhibited by the shell and it may be mentioned that no other abnormalities or pathological conditions have so far been met with in our experiments.

The form of spiral typical for this species is shown in Plate V, figs. (*a*)–(*h*). Variations from this type may take two main forms:

(i) Where the spiral is definitely dextral or sinistral but either (Plate V, figs. *l*, *m* and *n*):

(*a*) Scalariform, *i.e.* showing an irregular elongation of the spire and, in extreme cases, disconnection of the whorls (Plate V, figs. *n* i–ii).

(*b*) Unduly flattened so that the apex and the upper portion of the subsequent whorls lie almost in one plane (Plate V, figs. *l* i–iii).

(ii) Where the spiral is coiled completely on the flat so that the apex is intorted and it is not clear whether the shell is dextral or sinistral (Plate V, figs. *k* i–iv).

Typical scalariformity has only been met with in one adult, SS 779 (Plate V, figs. *n* i and ii), which occurred in the *E* brood from SP 114 (Table V) and itself gave rise to an *E* brood. Slight scalariformity of the upper whorls has been noted by Boycott in some of the young in the *E* brood from SS 679 (Table V).

The one odd dextral from SS 2184 (Table VI), although it died very young, showed marked scalariformity with disconnected whorls.

Of the remaining 20 cases recorded in Tables I–VI some relate to shells with flattened spires ((i) *b*) but more than half relate to completely flat-coiled shells with disconnected whorls (ii). Only six out of the twenty lived to reach maturity: five with flattened apices (Plate V, figs. (*l*), (*m*)), one completely flat-coiled (Boycott, 1922) with disconnected whorls (Plate V, figs. *k* i–iv). All six died without issue. The remaining records are from young shells that died shortly after hatching or even failed to hatch.

Young snails of this nature are recorded by Pelseneer (1920: see particularly his figures on pp. 352 and 353) for several species, including *Limnaea stagnalis*, but it is not possible from the information he gives to say whether his records support or refute the conclusion I have drawn from our more detailed evidence.

Of the 21 examples found by Boycott and myself two were recorded from two type *C* broods; ten were recorded from seven different *E* broods nine from nine *D* broods. With the exception of the *C* broods where, from the nature of the cross producing such broods, abnormality and failure of the embryos is not surprising, *every record except one comes from a first-*

cousin group where suppression is definitely in operation. The one record that cannot definitely be classed occurred in the 4th generation *D* brood from DS 2037 (Table VI). As this brood was the only one obtained in that particular group it is impossible to say whether suppression was present or not.

From the nature of the mechanism by which I have suggested that suppression operates, variations of this kind are to be expected in the groups in which they have been found. They may be loosely thought of as snails which, under the influence of two opposing forces, do not quite know which way to turn.

It might be said that if this explanation holds, the number of cases recorded by us is much too small. Against this must be set three facts:

(i) The apparently definite connection of large masses of addled eggs in groups where suppression is in operation.

(ii) The general body of evidence offered by other workers which supports the view that variations of this nature are more prevalent among embryos than adults; and that such individuals most frequently fail at an early stage in their development.

(iii) The fact that these variations are not readily detectable unless development has reached a certain stage and may even then be missed unless the capsules of addled eggs are very carefully examined (an operation which up to date has been carried out in very few cases).

In this connection it may be added that from a colony of *Helix nemoralis* at Bundoran, Ireland, over 2000 sinistral individuals have been taken at various times (Collier, 1913) and also a number of shells exhibiting varying degrees of scalariformity. Through the kindness of Mr J. R. le B. Tomlin I have been able to examine many of these shells. It is hoped that, by an intensive survey of this local race, we may be able to discover whether there is any definite connection in this case between these two forms of abnormality. Mr Tomlin also informs me that from the same area he has received sinistral and scalariform examples of *Helix itala*.

23. FECUNDITY OF ODD DEXTRALS.

Up to the end of 1922, 36 odd dextrals and 2 odd sinistrals had been obtained. During the 1923 breeding season these numbers were very considerably increased, but the results from these snails will not be available till the end of the 1924 season.

The two odd sinistrals died young. The 36 dextrals fall into two classes:

those undoubtedly derived from suppressed R parents and those probably derived from suppressed RL parents.

In the former class there are two broods:

SS 4501 (Table III) giving 8 sinistral and 5 dextral.
SS 331 (Table V) giving 9 sinistral and 4 dextral.

Four from 4501 unfortunately died young but the remaining five all bred on self-fertilization and gave 215 young, or an average of 43 per snail.

In the latter class there are 17 broods which together gave 27 odd dextrals; of these 5 died young and attempts were made to breed from the remaining 22 by self-fertilization:

14 died before maturity or failed to produce eggs or young;
1 gave only addled eggs;
7 gave together 31 young, or an average of 4 per laying snail.

Before considering these results it must be quite definitely stated that *the average figures for the two classes are not in themselves comparable.* It was necessary to make the division, as the behaviour of the two classes might be expected to be, and obviously is, different. In the former class four, bred by Boycott, were under optimum conditions and in the fifth case, bred by Burlend, suppression is apparently absent.

In the latter class the attempts were made by five different workers under average conditions and, if compared with the general results obtained by the same workers with other broods, it can be seen at once that the percentage of failures (over 60) is decidedly high, and the average number of young per laying snail is extremely low. Beyond this statement it would not be profitable to go on our information alone. It is, however, supported from another source.

In 1880 Call made a statistical examination of the occurrence of "reversed" *Melanthones* (*Campeloma*). In this group several dextral species persistently throw, in nature, odd sinistrals in a manner apparently quite comparable to that in which odd dextrals and odd sinistrals have occurred in our broods. The figures he obtained from a comparison of the number of odd sinistrals present at or about the time of parturition and of the number of adult sinistrals present in the population, disclose a very high percentage of snails of this type that failed to reach maturity. His method is one which, in the light of more recent genetical research, is open to serious criticism, but even when due allowances are made, his results are still significant. Arguing from the presence of embryos with abnormal shells, he is inclined to ascribe the presence both of these

abnormalities and of the odd sinistrals found with them to the effects of over-crowding and pressure on the eggs. Whether these abnormalities are in any way comparable to those found by us it is not possible to say, but their occurrence here is suggestive.

24. SUPPRESSED FIRST-COUSIN GROUPS.

If E and F broods are in reality suppressed A and D broods, then, on the general hypothesis, they should occur with predicable regularity in certain groups.

The occurrence of suppressed broods generally seems to be connected with strains that have been carried through two or more generations by self-fertilization: but they also apparently arise in the 2nd generation from a cross between a homozygote and a like heterozygote (*e.g.* L $\times$ LR) as in the London pair (Tables I and III) and possibly DP 48 (Table V).

As has been stated, the present evidence is mainly restricted, for a variety of reasons, to the behaviour of E broods; so that we might expect to find three out of the five possible first-cousin groups, namely, suppressed α, suppressed γ of the D–E type and suppressed δ, all of which have been obtained. The remaining groups, namely, suppressed β, suppressed γ of the A–F type and suppressed ϵ should arise in strains where the D broods are suppressed so as to appear as type F.

Since the main body of the experiment has only reached the 4th generation and since the predominant method has been the isolation of singles, this part of the enquiry must naturally depend mainly on evidence from suppressed γ groups derived from isolated single grand-parents. A large number of such groups are available, among them several of the A–F type. These latter should, and apparently do, behave in a manner precisely similar to that of the D–E type. Suppressed ϵ and, if the proper crosses are made, suppressed β groups should be obtained by carrying on to the next generation F broods and some of their sister broods of type A.

Suppressed α groups. Only one such group has been obtained so far. It occurred in the 5th generation from SS 331 (Table V). Of the thirteen broods all should appear as E or show other indications of suppression. Eleven broods are definitely type E and two appear as D. As was shown in Section 18 (Fig. 6) all the broods are relatively small and the proportionate occurrence of odd dextrals in the group is high. Other indications of suppression are also present. The presence of the two D broods cannot be regarded as significant, as both broods are quite small which, under the circumstances of this particular case, is presumptive evidence of the operation of suppression.

Suppressed δ *groups*. Both the possible representatives of this group-type are difficult to analyse. The figures for the 3rd generation from DP 48 have already been considered in Section 20. The 2nd generation from the London pair (Tables I and III) is complicated by the fact that so many pairs were set and there is not yet sufficient evidence to show how suppression affects the results of pairing. The following rough analysis is given for what it is worth:

Forty-seven snails of the 1st generation London family succeeded in depositing eggs and they may be classed under three headings:

	Probable L or LR	Doubtful	Probable RL
	30	9	8
Expectation based on assumption that the parent cross was L × LR ...	*35·25*	—	*11·75*

The doubtful column includes snails giving eggs all, or a considerable portion, of which were addled, singles giving broods of less than 10 and pairs giving broods of less than 20.

The behaviour of SP 36 (Table II) makes it just possible that the original parents of the London family were LR × LR in which case the expectation would be 23·5 : 23·5.

There are several other small groups which might possibly belong to this type, but their analysis would be of little value.

25. Suppressed γ Groups.

Owing to variations in the size of broods and in the degree of suppression, these groups are not easy to analyse with any accuracy even when due regard is paid to the evidence to be derived from low fecundity, addling of eggs and abnormal embryos. In the following argument I do not propose to deal with groups derived from paired grand-parents.

The 4th and 5th generation groups from DP 48 (Table V) provide very clear evidence supporting the general and special hypothesis. (A general discussion of this family will be found in the next section.) Proceeding on the asumption that the 2nd generation brood resulted from the cross L × a heterozygote, we should expect by self-fertilizing the individuals of the 3rd generation broods derived from singles to get suppressed γ groups from all the *E* and some of the *D* broods.

For the purpose of analysis the broods in this family may best be shown under five headings.

	D broods				
	Addling absent or insignificant				
	Broods over 10	Broods 10 and under	Addling considerable	Broods totally addled	Recognizable *E* broods with or without addled eggs
	(i)	(ii)	(iii)	(iv)	(v)
Boycott carried on the *D* brood from SS 102 and obtained five broods in the 4th generation ...	2	1	1	—	1
He again carried on the *D* brood from SS 330 (shown in col. (i)) and obtained 12 broods ...	7	—	—	1	4
Thus the totals are: *D* Doubtful *E* 9 3 5					
The general trend of the evidence makes it very likely that 2, if not all, of the 3 doubtful broods in reality represent suppressed broods					
Turner carried on *D* broods from					
SS 5006	1	2	—	1	3
SS 5008	2	1	—	—	4
SS 5012	3	1	—	1	3
and an *E* brood from					
SS 5007	4	2	—	—	3
and two odd dextrals from SS 5011 and SS 5015 ...	—	2	—	—	—
Turner, as has been stated above, in inclined to think the 2 broods in col. (iv) are not significant in this case					
Adams carried on a number of snails from 3 *E* broods bred by him in the preceeding season. For some, as yet undetermined, reason the percentage of failures was extremely high and the average number of young per laying snail extremely low, *i.e.* 5·7 (SS 3001, 3002 and 3004) ...	2	6	—	2	—
The absence of the expected *E* broods is therefore easily understood					
Mrs Bateson and I carried on a number of snails from the 3rd gen. brood SS 110	4	4	—	2	1
Again the percentage of failures was high and the average per snail laying in its first season was 12·6					
(Several of the failures were paired in their second season and gave equally small broods. One, SS 2068, layed on self-fertilization and gave 49 young. The pairs are not included here.)					
Four of these broods were carried on by us to a 5th gen. The conditions were improved and the results were better:					
SS 2047	2	—	—	—	2
SS 2063	—	2	—	—	1
SS 2058 gave 6 *D* broods, which probably represents the expected ϵ group, and the *E* brood SS 2065 gave 1 further *E* brood, which is not shown here as, although it probably represents a γ group, it cannot be definitely stated that it is not a suppressed α group.					
The total, then, for the 4th and 5th gen. γ groups of this family is	27	21	1	7	22

If total or considerable addling may be taken as indicative of suppression (disregarding the two doubtful cases) we get:

	D	Doubtful	*E*
	27	23	28
Expectation	*39*	—	*39*

It is manifestly impossible to say how broods containing less than 10 snails would have appeared had they been larger. Information as to the way in which odd dextrals are distributed in an *E* brood is scanty. At first there seemed to be evidence pointing to the operation of a time factor. In other words in such broods as came under observation the odd dextral was apparently among the first lot of eggs, and in the one *A* brood, breaking through in a suppressed group, that has been under my personal observation, the *young* were observed more than a month before the *eggs* of the nine sister broods were seen. Eight of these later appeared as *D* or *E* broods (DS 2026, Table VI).

A further point must not be overlooked. There is a slight danger that the shells of the snails in the early capsules that die shortly after birth may disintegrate before the brood is counted, and in this way some odd dextrals might be missed. On the other hand, one or two definite cases have been observed more recently where, at any rate, subsequent odds have appeared among the later capsules, and in the case of *E* broods in the SS 331 group (Table V), where the proportion of sinistrals to dextrals was almost as 1 : 1, the two types were apparently evenly distributed.

In spite of this I am inclined to think that further evidence may support the idea of a time factor, which would not be at all inconsistent with the general idea underlying the hypothesis of suppression. It is for this reason, therefore, that I have drawn the arbitrary line dividing the *D* broods as low as 10 on the size scale.

Two groups appeared in the 4th and 5th generations of the DP 50 strain (Table VI). The first was bred by Turner from DS 5019 and consisted of:

A broods		Totally addled broods	Suppressed broods	Apparent *D* broods	
Over 10	10 and under			10 and under	Over 10
3	2	4	1	2	—

The group is an unsatisfactory one in that the four broods totally addled, although their occurrence here might be expected, are strongly suspect by Turner owing to the possibility of the interference of high water temperatures: added to this, three of the broods contained only one snail each. The appearance of the brood given by DS 5108 is difficult

to understand, although a possible explanation presents itself. A sister group also reared by Turner from DS 5020 gave an apparently normal γ group.

The 5th generation group reared from DS 2026 by Mrs Bateson and myself is not open to this suspicion. The dextral parent on self-fertilization gave an all sinistral brood which, carried on also by self-fertilization, gave:

D broods					
Over 10	10 and under	Containing abnormal young	Broods totally addled	Suppressed broods *E*	Unsuppressed *A*
3	2	2	1	1	1

Or:

	D	Doubtful	*A* or suppressed *A*
	3	4	3
Expectation	*5*	—	*5*

The general trend of the evidence seems to show that two at least of these doubtful broods should be grouped with suppressed *A*, *i.e.* those containing abnormal shells. It will be seen that the *E* brood also contained abnormal shells. This group is also of importance in that it is one of the three groups which plainly show the impossibility of interpreting these results on the assumption of only one class of heterozygote. The sister group from DS 2028 gave, as might be expected, a fairly clear ϵ group containing six *D* broods all over 10.

The only other groups in the Radlett family are the 3rd generation group from SS 122 and the 4th generation group from SS 263 (Table IV). These groups, immediately derived as they are from the dextral individuals of an *A* brood, show the reverse position in that suppression operates on the *D* broods which therefore appear as *F*:

	A broods over 10	Suppressed *D* broods, *F*
	9	4
Expectation	*6·5*	*6·5*

There is a shortage of suppressed broods here, but in this connection it must be stated that the SS 263 group was among those reared by Boycott under optimum conditions and in spite of this two snails failed to give eggs or young.

The London family contains a number of 4th generation groups in which the definite 1 : 1 formation of a suppressed γ group is expected. In order to avoid error, only groups derived from an *isolated single grand-parent* have been considered.

(Table I).

1st gen. ref. no.	2nd gen. ref. no.	3rd gen. brood-type	*D* broods: Over 10 (i)	*D* broods: 10 and under (ii)	*D* broods: Addling considerable (iii)	Broods totally addled (iv)	Broods of type *E* (v)	Unsuppressed *A* (vi)
SP 34	SS 259	*E*	4	1	—	—	1	—
SP 39	SS 226	*D*	8	2	1	1	1	—
SP 39	SS 229	*D*	4	—	1	—	1	—
			16	3	2	1	3	—

From these groups, all reared by Boycott, on the best interpretation we get a considerable shortage of suppressed broods.

	D	Doubtful	Suppressed *A* or type *E*
	16	3	6
Expectation	*12·5*	—	*12·5*

(Table III).

Two further 3rd generation groups, the broods of which were reared by Burlend, Rathbone and Poole, come into this class, and one 4th generation group reared by Thornton.

	1st gen. ref. no.	2nd gen. brood-type	(i)	(ii)	(iii)	(iv)	(v)	(vi)
	SS 17	*D*	—	—	—	—	1	1
	SS 12	*D*	3	2	—	—	1	1
	2nd gen. ref. no.	**3rd gen. brood-type**						
	SS 326	*D*	3	—	—	—	1	—
From one of the *D* broods of the SS 12 group a 4th gen. group was reared by Boycott (under optimum conditions)	SS 4111	*D*	8	1	—	—	6	—

Under the circumstances the 1 brood in col. (ii) containing only 3 young is undoubtedly significant; added to this one parent is recorded as giving no eggs or young.

From these families we get:

	D broods	Doubtful	*A* or suppressed *A*
	14	3	11
Expectation	*14*	—	*14*

(Table II).

We are now left to consider the important but complex 4th generation groups reared by Boycott from SP 36. The difficulty of analysis here is chiefly due to the fact that the general argument on the composition of the family is, and must at present remain, inconclusive (Sections 11 and 27). The 12 groups fall into four categories.

(*a*) One appears as a normal unsuppressed γ group and has been considered under that heading.

(*b*) Three at present exhibit no clear evidence of being derived from a heterozygous grand-parent and will not be analysed here.

(*c*) Four show suppression of *D* broods.

(*d*) Four show suppression of *A* broods.

(An (R) before the reference number indicates that the group was among those treated to optimum conditions.)

Where *D* broods are suppressed:

	2nd gen. ref. no.	3rd gen. brood-type	*A* broods: Over 10	*A* broods: 10 and under	*A* broods: Addling consider-able	Broods totally addled	Sup-pressed *D* or *F*	Unsup-pressed *D*
(R)	DS 279	*A*	8	—	—	1	1	—
	DS 290	*A*	3	—	—	1	—	1
	DS 300	*A*	14	—	—	—	—	1
(R)	SS 4103	*A*	9	—	—	—	2	1
			34	—	—	2	3	3

Where *A* broods are suppressed:

	2nd gen. ref. no.	3rd gen. brood-type	*D* broods: Over 10	*D* broods: 10 and under	*D* broods: Addling consider-able	Broods totally addled	Sup-pressed *A* or *E*	Unsup-pressed *A*
	DS 297	*D*	4	4	—	1	1	—
(R)	DS 301	*D*	12*	—	1	—	1	—
	SS 275	*D*	6	2	1	—	1	—
(R)	SS 4102	*D*	15	—	—	—	1	—
			37	6	2	1	4	—

* One of these broods contained an abnormal shell which makes it likely that in reality it is a suppressed brood.

One thing, indicated by the other figures, is clearly confirmed in these two tables, namely, *that suppression in its inception operates in favour of the type of spiral exhibited by the parent animal.* In this connection I have purposely refrained from using the words "mother" or "maternal." Confusion of thought is bound to arise from identifying an hermaphrodite self-fertilizing animal with one sex rather than the other.

Further there is no substantial difference in the behaviour of the suppressing force whether it operates in favour of one type of spiral or the other. The two categories may therefore be considered together, which gives:

	Broods of parental type	Doubtful	Opposite type suppressed or "breaking through"
	70	6	16
Expectation	*46*	—	*46*

The shortage of broods recognizably suppressed or breaking through is marked.

These figures, reduced to percentages, may be compared with those from the DP 48 groups and those from the other isolated groups throughout the experiment.

Family	No. of broods	Broods of parental type	Doubtful	Opposite type suppressed or "breaking through"
(*a*) DP 48	78	34·6	29·5	35·9
(*b*) Other families	88	51·1	15·9	33
(*c*) SP 36	92	76·1	6·5	17·4

(The figures in the last column include broods recorded as having abnormal young and considerable or total addling, except where this is of doubtful significance.)

The figures suggest that (*a*) and (*b*) are probably similar and that (*c*) may be dissimilar. All things considered, the figures for (*a*) and (*b*) are not unreasonable on the basis of the special hypothesis, but the figures for (*c*) have a marked divergence from expectation. This may mean one of two things, either that a different genetical system is operative in the SP 36 group, which seems hardly likely, or that the force of suppression is relatively stronger here than elsewhere, which, in view of the variation in this respect shown by different populations in nature, is at least feasible. (The possibility that in our stock *fresh* sinistral or dextral mutants may arise has not been overlooked.)

Considered generally the results of this examination of 258 broods tend further to confirm both the general and special hypothesis; and there seems little doubt that these groups are in fact but a special case of the 1 : 1 brood ratio so plainly seen in those groups where suppression is absent.

26. General Analysis of the DP 48 Family. (Table V.)

It has been shown that the constitution of the two snails used to make this pair was probably L × a heterozygote. A definite statement, however, must await the solution of the problem of type *B* broods. If, pending this, we assume that one animal was L the other might have been LR, suppressed RL, or even possibly normal RL. Under these circumstances the appearance of *E* broods in the 3rd generation is not unreasonable and the 2nd generation brood should be a normal *D*. In point of fact this brood was composed of 137 normal, and one slightly abnormal, sinistrals. This result makes it just possible that suppression may have been already operative in one of the parents. The analysis of the broods from the 42 sister snails to this pair (Table IV) shows the probable number of snails with

Dextral determiners	Sinistral determiners	Suppressed dextral
20	21	1

The expectation if suppression were absent is fulfilled. The sudden appearance, then, of the definite E brood SS 72 becomes difficult to explain. The general size of the broods throughout the group is reasonably large. No other evidence of abnormal shells exists. The four cases of partial addling reported by Garstang cannot be regarded as significant. In fact none of the evidence usually connected with the incidence of suppression is present. Beyond this we cannot go.

Whether or not suppression was already operating in the 2nd generation brood, it appears in the 3rd generation in a perfectly definite form. The six E broods from singles have the appearance of being derived from suppressed RL parents, and their behaviour, in so far as they were carried to a 4th generation, as shown in Section 25, tends to confirm this. Of the D broods 1/3 should give suppressed γ groups in the 4th generation. Six of these were carried on and, contrary to expectation, five gave typical suppressed γ groups while only one gave an ϵ group. Two of these suppressed γ groups have now reached the 5th generation. In the first case a D brood 330 gave a typical suppressed γ and the E brood 331, as was to be expected from its appearance, gave a suppressed α group. In the second case three D broods and one E were taken on; here the expectation of suppressed γ groups from D broods is 1/2, actually two suppressed γ groups appeared and one ϵ. From the E brood only one brood was obtained, which was also E. This might represent a suppressed γ or a suppressed α group. The chances are equal.

Thus throughout the 3rd, 4th and 5th generations this family undoubtedly follows the main principles underlying both the general and special hypotheses.

27. General Analysis of the London Family. (Tables I–III.)

It has been shown from a rough analysis of the 2nd generation group that the original London pair were probably of constitution L and LR. If suppression were not operative, we should expect from setting 16 pairs from the 1st generation D brood to obtain:

A	B	C	D
1	2	—	13

That is assuming that the cross L × RL gives a normal D brood. Thus 3/16 broods should show dextrals; it is, therefore, not unreasonable to expect that when suppression is present 3/16 broods would show signs of the suppression of their dextral nature.

From the 1st generation brood, 17 pairs were set (Table I) and taking the broods at their face value the results were:

	D	*E*
	13	4
It will be remembered that in DP 48 (Table V), which was probably of similar composition, 7 pairs were set giving	5	2
	18	6
Expectation	*19·5*	*4·5*

As that stands the expectation is reasonably fulfilled, but it cannot be overlooked that there are no less than six of the *D* broods under 20 and SP 38 (Table I) shows the presence of an abnormal shell; against this must be set three facts:

(i) That 4/13 of the *D* broods should arise from the cross L × RL and its reciprocal and, *ex hypothesi*, the RL individual should show a low fecundity.

(ii) That in the early days of the experiment the best methods of maintenance were not so well known.

(iii) The probable excess of RL snails used among the London family pairs is in part counter-balanced by the fact that no *E* broods resulted from the 13 snails set as singles, though in SS 8 (Table III) the total failure of eight capsules of eggs is probably significant as is also the result from SS 15. Allowing the first case, we get:

	D	*E* or probable *E*
London family (Table III)	12	1
DP 48 (Table V) ...	17	6
	29	7
Expectation	*27*	*9*

So far, then, as the 2nd generation group is concerned, the results do not disagree with the suggestion that the original parents were of constitution L and LR.

If this be accepted certain conclusions must follow regarding the behaviour of the 3rd and 4th generations:

(i) Among the pairs (Table I) giving *D* broods the chances are that 4/13, or approximately 1/3, would show a pure sinistral line: the remaining 2/3 should exhibit their impurity by the appearance of odd dextrals in the 3rd or 4th generations. Five of these broods were carried on:

SP 44 gave only one 3rd generation *D* brood, so here no argument is possible.

SP 34 and SP 39 show definite evidence of impurity.

SP 3 shows presumptive evidence of impurity.

While in SP 27 fourteen snails were successful in producing 3rd generation broods, giving a total of 976 sinistral young. It seems clear, then, that this is the expected pure line. It is unfortunate that this group could not be carried on to the next generation.

(ii) The pairs giving *E* broods (Table I) should *all* show impurity of strain in the 3rd generation. Two out of three of the undoubted *E* broods (SP 36 will be separately dealt with) were carried to a 4th generation. SP 5 gives a reasonable result, but SP 26 does not. The probable expectation in this latter case would be a suppressed γ group in the 3rd generation, with *D* broods giving further suppressed γ groups in the 4th generation. The only indications in this big group, involving 1208 snails, are the two abnormal shells in SP 119 (3rd generation) and SS 420 (4th generation). Only one explanation of this result seems possible. It may be argued that the appearance of only one odd dextral in a brood containing 145 snails indicates that the suppressing force is unduly strong (the same position is found in the sister brood (SP 28) where one odd dextral occurs in a brood of 163), and further that these broods have behind them three and four *known* generations of sinistral parents. It has already been shown that the incidence of suppression in the London family is inclined to be erratic. In some places it appears to be strong, while in others it has been partially or completely broken down. Such an explanation, though probably correct, cannot yet be frankly accepted as representing the actual facts and the solution of this particular problem must await further evidence.

(iii) The curious 2nd generation brood from SP 36 (Table II) probably arises from the cross RL × RL (which would be expected once in sixteen times), where, as is not unreasonable from the nature of the cross, the suppressing force has largely been broken down. In Section 11 the history of this pair has been given and it was suggested that this might represent a type *C* brood, resulting from the cross R × L and its reciprocal. (If this were so the original London pair must both have been LR in constitution, which, considering the London family as a whole, makes a much poorer fit.) In either case a γ group would be expected in the 3rd generation and this is found. In the 4th generation the expectation differs. If SP 36 was R × L, *all* 4th generation groups should be type γ. If RL × RL, some α and some ϵ groups should appear, while the remainder should be γ. The twelve 4th generation groups have been partially analysed on p. 185, where it was shown that eight and probably nine of them are of type γ, all except one showing a marked

degree of suppression: of the remaining three apparently one is an α group and two are ϵ.

If in reality these groups are what they appear to be the possibility of SP 36 having been R × L is ruled out. The results from the five pairs, though some broods are small, are also more in accordance with the RL × RL expectation. Further breeding alone, however, will provide a definite answer.

(iv) Since the singles apparently all gave *D* broods, about 1/3 of these broods should give impure strains. Table III shows that three lines are definitely impure and one line is probably pure. The remaining broods have not been carried on in sufficiently large numbers for analysis. The groups derived from SS 12 give a very clear example of the behaviour of an isolated single of constitution LR.

Thus considered as a whole this family also shows a reasonable degree of conformity with the principles underlying the general and special hypotheses.

28. Summary of Evidence relating to the Special Hypothesis of Suppression.

It was seen early in the experiment that two types of mixed broods, referred to as *E* and *F*, were occurring both from pairs and singles in an apparently irregular manner. An examination of our results based on the general hypothesis revealed that under certain conditions there was a definite shortage, or entire absence, of the expected *A* or *D* broods and that *E* or *F* broods appeared in their stead. It therefore seemed that such broods and groups might arise from the suppression or modification of the normal system of inheritance underlying the general hypothesis.

The evidence relating to this problem may be summarized as follows:

(i) The examination of first-cousin groups where suppression is operating shows that in most cases either all the *A* broods are absent and are replaced by *E*, or all the *D* broods are absent and are replaced by *F*.

(ii) In some cases an *A* brood appears in the same group with *E* broods or a *D* brood with *F*. In other words the force of suppression is either partially absent or in certain cases overcome.

(iii) In its inception suppression seems to operate in favour of the type of spiral predominantly exhibited by the parental strain.

(iv) It seems to arise most frequently as the result of continued self-fertilization or from pairs where one animal is heterozygous, but both determine the same type of spiral (*e.g.* L × LR).

(v) Odd dextrals or odd sinistrals give the same types of broods as are to be expected from their sinistral or dextral sisters.

(vi) *E* broods thus seem to represent suppressed *A* broods, and conversely *F* broods represent suppressed *D* broods. Consequently, the two types behave in the same way.

(vii) First-cousin groups are found of the same types as are to be expected from the general hypothesis, *i.e.* suppressed α groups (all *E* broods instead of all *A*); suppressed δ groups ($3D : 1E$ instead of $3D : 1A$); suppressed γ groups (in this case of two types in accordance with the type of spiral the appearance of which is suppressed $1D : 1E$ or $1A : 1F$). Suppressed groups of type β ($3A : 1F$) and ϵ (all *F*) have not yet been obtained as they involve further breeding from γ groups of the *A–F* type, which has not yet been done.

(viii) Both in groups subjected to improved conditions, and throughout the experiment generally, the numbers of young per brood in *A* and *D* broods are on the average definitely larger than the numbers in *E* and *F* broods.

(ix) The early failure, or addling, of all, or a greater part, of the eggs laid seems to be definitely associated with groups in which *E* or *F* broods occur.

(x) The incidence of abnormal shell-coiling seems to be similarly associated, but the evidence for this association is not so clear.

(xi) The fecundity of the odd dextrals themselves seems to be relatively lower than that of other snails, and it is possible that their hold on life is weaker.

(xii) *E* and *F* broods decrease in size in inverse proportion to the number of odd dextrals or odd sinistrals present.

(xiii) Where on the general hypothesis an α group is expected, but is actually suppressed, all broods are relatively small and the proportion of odd dextrals is high.

(xiv) Where the force of suppression is either absent or completely overcome normal fecundity results.

(xv) *E* and *F* broods fall into at least two, and possibly more, classes, but the figures at present available are insufficient for a definite statement.

(xvi) Apart from this the degree of suppression seems to vary as between different groups and families.

(xvii) It seems possible that the degree of suppression may vary directly with the number of preceding generations which have a similar coil.

(xviii) It seemed possible that the ratios of sinistrals to dextrals in *E* broods and *vice versa* in *F* broods might fall into a definite series, but, owing to the small size of the broods and the chances of experimental error, the figures although suggestive form at present insufficient basis for a statistical argument.

(xix) There is definite evidence of the existence of (at least) two types of heterozygote (LR and RL).

(xx) Heterozygous strains throughout the experiment seem to be more prevalent than would be expected if only a single pair of factors were involved. No analysis on the basis of more than one pair of factors has been attempted at this stage, as in any case the principle is the same, and such an analysis would only add further complications to an already overcomplicated problem.

(xxi) The general analysis of the London family and the DP 48 groups through four generations agrees with expectations based on the special hypothesis, and thus these families represent a suppressed variation of the same system of inheritance underlying the general hypothesis.

(xxii) From this evidence we can only conclude that *E* broods are in fact suppressed *A* broods and that *F* broods are in fact suppressed *D*.

29. Special Hypothesis.

If the general hypothesis can be accepted then the determination of the pattern of an individual rests upon the interaction of the parental nuclear factors (which segregate in a normal manner) and the existing modification imposed on the germinal structure of the parent by the action of the nuclear factors of the preceding generation. That is, the nuclear factors of the parent have been brought to bear upon the germinal structure which determined this parent's pattern and, in accordance with their composition, have confirmed or changed this germinal structure, thereby determining the pattern of the offspring.

If this be so, it is not difficult to see that, by selected pairing or continued self-fertilization, one type of germinal structure may become so strengthened or confirmed that it is capable of resisting, partially or completely, any effort to change it exerted by the nuclear factors. On the other hand it is equally conceivable that by selective breeding this strengthened position may be broken down by the continued application of nuclear forces directed towards its change.

When the germinal structure is incapable of resisting the forces exerted by the nuclear factors the determination of the symmetry of

cell division will not be in doubt and the alternating (or "normal") type of inheritance expected on the general hypothesis will result.

When the germinal structure has been strengthened by selective breeding, isolation and time (measured by generations) so that it can offer *complete* resistance to the forces exerted by the nuclear factors, again the symmetry of cell division will not be in doubt, and an *apparently* pure race will result. This apparently pure race may mask a considerable mixture of nuclear types which will only reveal their presence through some fortuitous series of matings resulting in the occasional appearance of inverse individuals. If selective breeding is enforced either by experimental control or the operation of natural isolation barriers and the like, the resistance of the germinal structure to change may be weakened. As this resistance weakens in relation to the forces exerted by the nuclear factors, so the determination of the symmetry of cell division in individual cases comes more and more into doubt, and the appearance of inverse individuals becomes more and more frequent, until ultimately through the breakdown of all resistance we may again find ourselves in the presence of alternating inheritance.

30. EVIDENCE FROM NATURAL POPULATIONS.

Pelseneer (1920, pp. 732–747) has devoted considerable attention to the problem of inverse symmetry and has collected together all the available evidence. The results of his researches into the state of affairs existing in natural conditions confirm the results of our experimental work on two fundamental points.

(i) That there are no morphological differences that can possibly separate the odd sinistral, occasionally found in species that typically exhibit the dextral habit, from the sinistral individual of a typically sinistral species; and the reverse relationship of the odd dextral to the typical dextral is precisely similar. It has been found both by Boycott and other workers that, whether found in our experiments or free in nature, all odd dextrals or odd sinistrals examined have shown complete inversion, and that this inversion is of the same morphological nature from the start. Drummond (1902) records an inverse embryo in *Paludina vivipara*, a dextral species recorded as giving odd sinistrals (*cf.* for *P. contecta*, Standen, 1905 and 1907). Pelseneer (p. 303) found in *Pterotrachea mutica* a clutch of eggs that were developing inversely. Lastly, Zur Strassen (1896) working on *Ascaris megalocephala* found about 1 egg out of 30–40 developing inversely, while among adults he found 4 showing inverse symmetry out of 125.

(ii) That the unity of the whole problem of inverse symmetry is demonstrated by the fact that a continuous series is to be found linking up in all possible grades typically dextral races which very rarely give odd sinistrals with typically sinistral races which very rarely give odd dextrals.

The main terms in this series may be exemplified as follows: Dextral species in which inverse forms are extremely rare or as yet unknown (*Ena obscura*, *Helix cantiana*, *Littorina littorea*, etc.): those in which odd sinistrals are less rare (*Helix pomatia*, *Helix pisana*, etc.): those which besides odd sinistrals have in one or more colonies established a sinistral "race" mixed with a dextral population (*Helix aspersa*, La Rochelle; *Limnaea stagnalis*, Aerschott; *Limnaea peregra*, Leeds, Heselden, Weidikon; probably *Helix nemoralis*, Bundoran). Pelseneer (pp. 30–36) lists 193 typically dextral species for which odd sinistrals have been recorded.

From this the series runs into those forms which Pelseneer groups as "permanently amphidromic." This condition may be seen, for instance, in those species which, though mainly dextral, are in a *part* of their area of distribution *typically sinistral* (*Chondrula quadridens*, *Pupoides pacificus*, *Eulota mercatoria*, *Bulimus purus*, etc.); or show *mixed* populations *throughout* their area of distribution (*Campeloma* spp., *Partula* spp.); and so on till we find species, like *Partula otaheitana*, which within the ambit of a single species, exhibit the complete series from dextral races giving odd sinistrals, through mixed populations, to sinistral races giving odd dextrals (Crampton, 1917).

Further terms in the amphidromic portion of the series are exhibited in many genera (*Achatinella*, *Amphidromus*, *Ariophanta*, *Orthalicus*, *Limnaea* (Hawaian spp.), *Bulimus* (*reversalis*, *candelaris*), *Pupoides* (*contrarius*), *Clausilia* (*fussiana*, *leucostigma*, *straminicolis*), *Fulgur* (*perversum*, *carica*), etc.).

Through these forms we are led to typically sinistral species for which odd dextrals have been recorded. Of these Pelseneer (pp. 36–37) lists 18 species (*Clausilia*, *Physa*, etc.).

This state of affairs is not difficult to understand in view of the results of selective breeding shown in Tables I–VI. The race of *L. peregra* from the Leeds pond, if dispersed to form new races under the action of natural isolation barriers, might readily give rise to precisely that state of affairs found in *Partula* to-day.

The lists of species for which sporadic inversion has been recorded comprise practically all the well known groups, and there is no reason to

doubt that, as our knowledge advances, these lists may be considerably increased.

We must not lose sight of the fact that the examination of such records of natural populations, unsupported by experimental work, may be misleading. The case of *Helix nemoralis* at Bundoran may be taken as an instance. Over 2000 sinistral shells, practically all dead, have been recorded from this area. On the face of it this looks like evidence of a definite sinistral race. Against this must be set the fact that the *H. nemoralis* population in such an area is enormous, and 2000 dead shells found in a closely worked area may in reality be the expression of a rare tendency to give odd sinistrals prolonged through a considerable period of time (Welch, 1900 and 1902). Experiment alone can decide whether this case should be classed with the verified sinistral races of *H. aspersa*, *L. stagnalis* and *L. peregra* or not.

This rare, but persistent, occurrence of inverse forms through a wide range of species is naturally capable of more than one explanation. Such variants may be, and freely have been, regarded as errant forms or strays of no genetical significance, due possibly to such external causes as overcrowding among the developing eggs. Considered individually, previous experimental efforts to solve this problem have lent support to this view. Several attempts have been made with odd sinistral *H. pomatia* by Lang (1896) and Künkel (1903). Taken together with the earlier work of Chemnitz, there are more than 30 records of progeny from such snails. As self-fertilization apparently is not practicable in this species, these workers proceeded by pairing sinistrals with sinistrals, and the numerous offspring were *all dextral*. De Witz (1916) worked with odd sinistrals of *Limnaea palustris* and also obtained only dextral young. With sinistral *H. aspersa* other workers (see Pelseneer, 1920, p. 656) obtained the same results.

In all these cases the animals used were odd sinistrals occurring relatively very rarely in a large dextral population. Our experiments have clearly shown that the chance of obtaining further sinistrals from such snails is not greater than, but equal to, the chance of getting sinistrals from their dextral brethren.

We know, roughly, the rarity of this latter event, and the results obtained are only to be expected in races, which, on our hypothesis, exhibit suppression to a very marked degree. The figures quoted by Pelseneer from several authors for the occurrence of odd sinistrals in a dextral race or *vice versa* give only the roughest idea of the likelihood of this event, but they are obviously analogous to the populations derived

from several of our groups: *e.g.* 4th generation groups from SP 36 (Table II):

DS 279 1 sinistral in a dextral population of 2327,

DS 301 1 dextral in a sinistral population of 3840,

and further they lend support to the view that suppression varies in different races whether within a single species or as between different species. The former phenomenon is well exemplified by the evidence from *H. aspersa*. Besides the results quoted above, there are further records that indicate a weakening of the force of suppression in this species. Daniel (1874), after many years of search, found three sinistrals in the same season near Epsom. Jeffries (1860) quotes the fact that a sinistral race was bred for many years in a garden at La Rochelle; and finally there is evidence of an all sinistral brood "breaking through." Johnstone (1850) refers to a French naturalist who obtained a complete sinistral brood "which he sold to advantage"! The latter position is exemplified by the relative frequency of odd sinistrals as between such species as *Littorina littorea* and *H. pomatia* or species of *Campeloma*.

The figures given by Call (1880) for *Campeloma* are precisely analogous to those obtained by us in, say, the DP 48 strain (Table V) only differing in the fact that the suppressed *Campeloma* broods are type *F* and not type *E*. Further, he has clearly demonstrated that such *F* broods, as we expected and have found in the reverse case, may be obtained from the odd sinistrals as well as from their dextral brethren. The same state of things clearly exists in some of the races of *Partula otaheitana*. For example, the figures given by Crampton (1917) for var. *sinistrorsa* in the Titaviri and Tenairi valleys show that, although the population is more or less equally divided between the two phenotypes, the number of gravid snails giving the opposite type of young is very small.

The work on *Partula* is so well known and has been given by Crampton in such detail that it would be tedious here to enter into a further analysis of these results. As the figures have been published, it is sufficient to say that, so far as suppression is concerned, this case does not appear to differ in any way from that which we have found in *Limnaea* and that which the evidence briefly reviewed above reveals as a general condition throughout Mollusca.

On the general hypothesis, this would indicate that there is a regular tendency towards the production of mutations involving the inversion of symmetry, and that these mutations would arise in the causative nuclear factors, but they would meet with, and usually be overwhelmed by, the force exerted by the organization of the germ cell which already has a strongly dextral or sinistral habit.

31. CONCLUSION.

It is not claimed that the general hypothesis or its special application, outlined in this paper, can yet be considered as proven; but it is contended that our combined results, here given in their entirety, show an encouragingly close agreement with theoretical expectation and a marked absence of unaccountable developments; and further that they form an adequate basis for preliminary judgment. Lastly the system of inheritance into which the general hypothesis leads us, although in its application it may seem intricate and unduly complex, is in its essence simple and is founded on a not unnatural conception.

In conclusion, I desire to take this opportunity of thanking the Rev. H. Poole and Mr G. C. Robson for their helpful criticism in certain sections of this paper, and Mr Osterstock for photographing the shells. I am also indebted to numerous friends for assistance at various times.

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PEDIGREE TABLES.

Table	I.	London family.	
,,	II.	,,	(SP 36).
,,	III.	,,	(1st generation "singles").
,,	IV.	Radlett family.	
,,	V.	,,	(DP 48).
,,	VI.	,,	(DP 50).

EXPLANATION OF SIGNS USED.

Numbers in small type above the line are reference numbers, those below in larger type show the number of snails in the brood.

Lines, reference numbers and brood numbers indicate:

When in *red* that the snails were *dextral* in appearance.
,, *black* ,, ,, *sinistral* ,,

¦¦	indicates a	dextral pair	referred to in text as			DP.
||	,,	sinistral ,,	,,	,,		SP.
¦	,,	dextral single	,,	,,		DS.
|	,,	sinistral ,,	,,	,,		SS.

The number of young shown below a pair is the total brood derived from both parents, except in the following cases:

–||	indicates	that the snail was paired and then isolated.
–|–	,,	that the snails were paired and the broods derived from each kept separate.
–?|	,,	a sinistral paired to a dextral in which effective fertilization was doubtful, the dextral only giving eggs.
+ |	,,	the presence of an odd dextral.
+ 1*m*	,,	,, ,, abnormal sinistral shell.
+	,,	that there is a significant record of addled eggs.
? +	,,	that addled eggs were recorded, but that the record probably has no significance: either there were relatively few eggs addled, or external causes may have operated.

DESCRIPTION OF PLATE V.

Figs. (*a*)–(*h*). Normal shells, natural size.

(*a*) Dextral (Table II).
(*b*) Sinistral (Table V).
(*c*) Dextral (Table IV).
(*d*) Sinistral (Table V).
(*e*) Dextral (failed to breed).
(*f*) Sinistral (Table I).
(*g*) Dextral (Table II).
(*h*) Sinistral (Table V).

Figs. (*k* i, ii, iii). Abnormal flat-coiled shell with disconnected whorls (enlarged 3 times). See Text, Section 22.

Figs. (*l* i, ii, iii) and (*m* i, ii, iii). Two abnormal sinistral shells where the spiral is unduly flattened, so that the apex and the upper portion of the subsequent whorls lie almost in one plane (enlarged 3 times).

Fig. (*k* iv). The same flat-coiled shell as above (enlarged 5 times).

Figs. (*n* i) and (*n* ii). An abnormal scalariform shell showing partial disconnection of the whorls; this snail occurred in the *E* brood given by SP 114 (Table V) and itself gave an *E* brood (natural size).

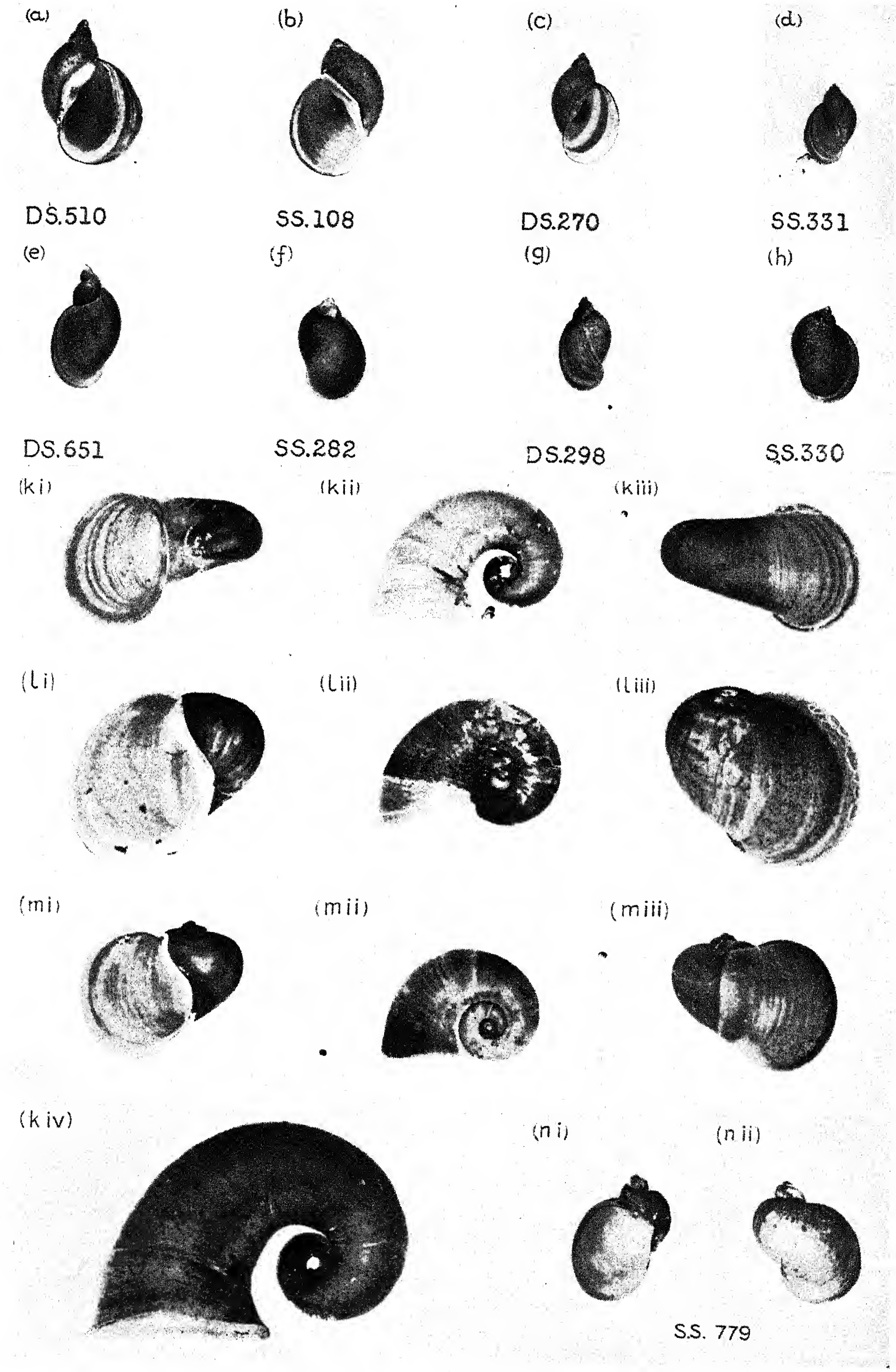

(a) DS.510
(b) SS.108
(c) DS.270
(d) SS.331
(e) DS.651
(f) SS.282
(g) DS.298
(h) SS.330
(k i)
(k ii)
(k iii)
(l i)
(l ii)
(l iii)
(m i)
(m ii)
(m iii)
(k iv)
(n i)
(n ii)
SS. 779

TABLE I.

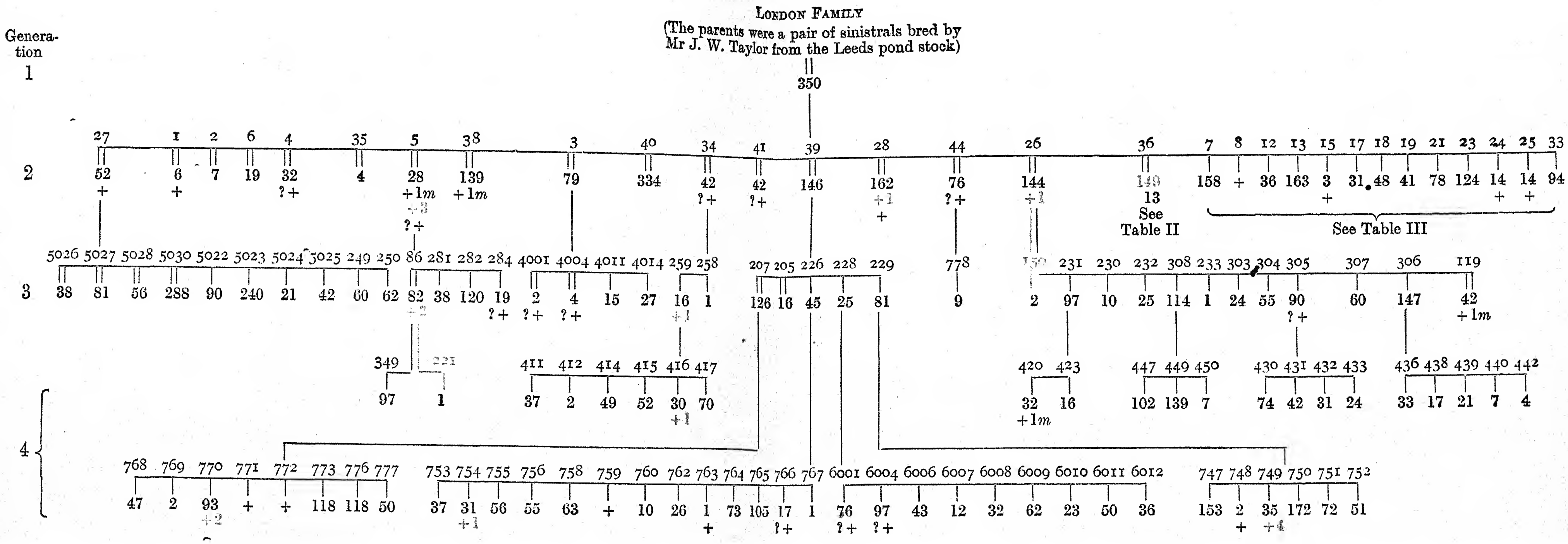

London Family
(The parents were a pair of sinistrals bred by Mr J. W. Taylor from the Leeds pond stock)
Generation
1
2
3
4
See Table II
See Table III

TABLE II.

London Family (SP 36).

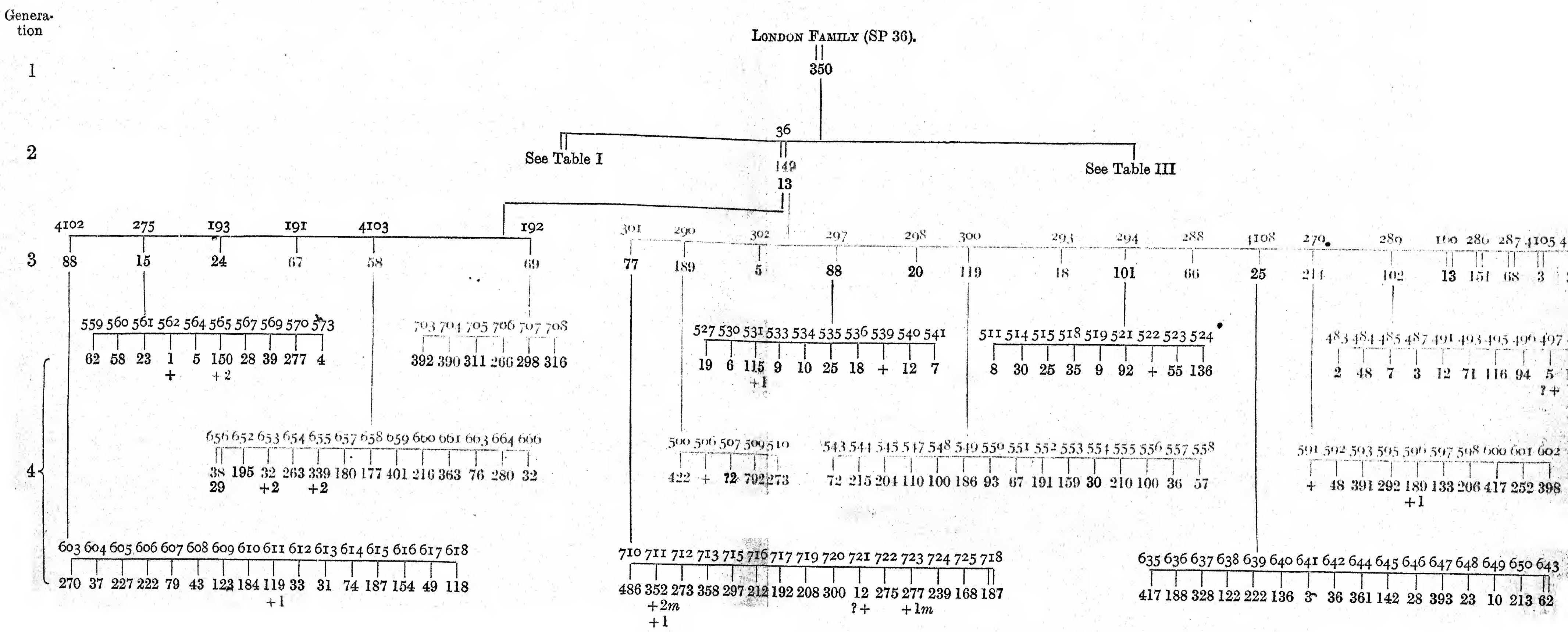


TABLE III.

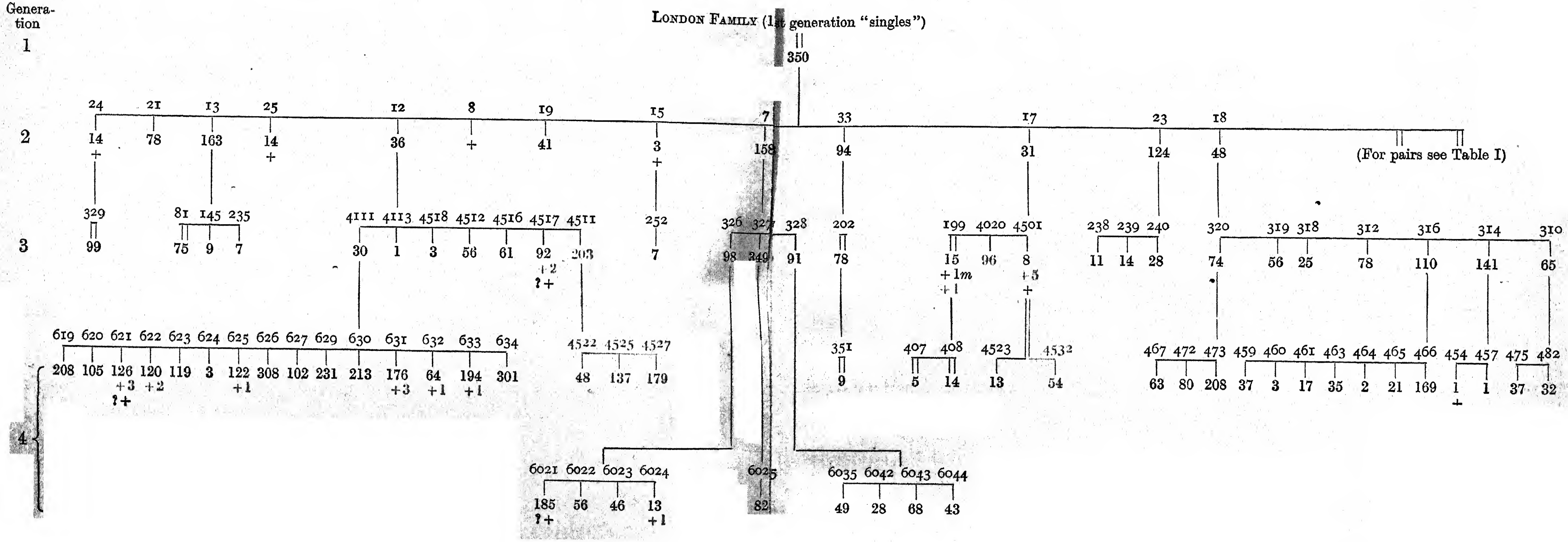
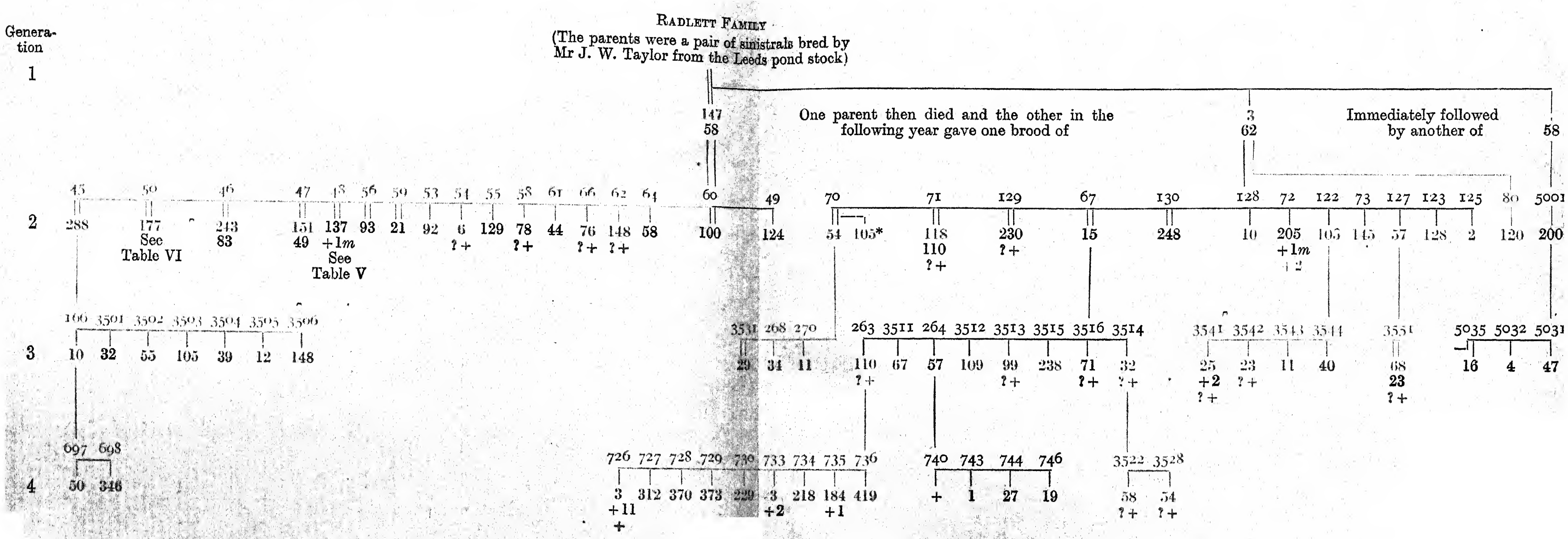

Generation
London Family (1st generation "singles")
(For pairs see Table I)

TABLE IV.



NOTE. The records of addled eggs in this table are, with the exception of those from 726 and 740, of very doubtful significance.

* One parent died and in the next season the remaining parent gave this brood.

TABLE V.

RADLETT FAMILY (DP 48)

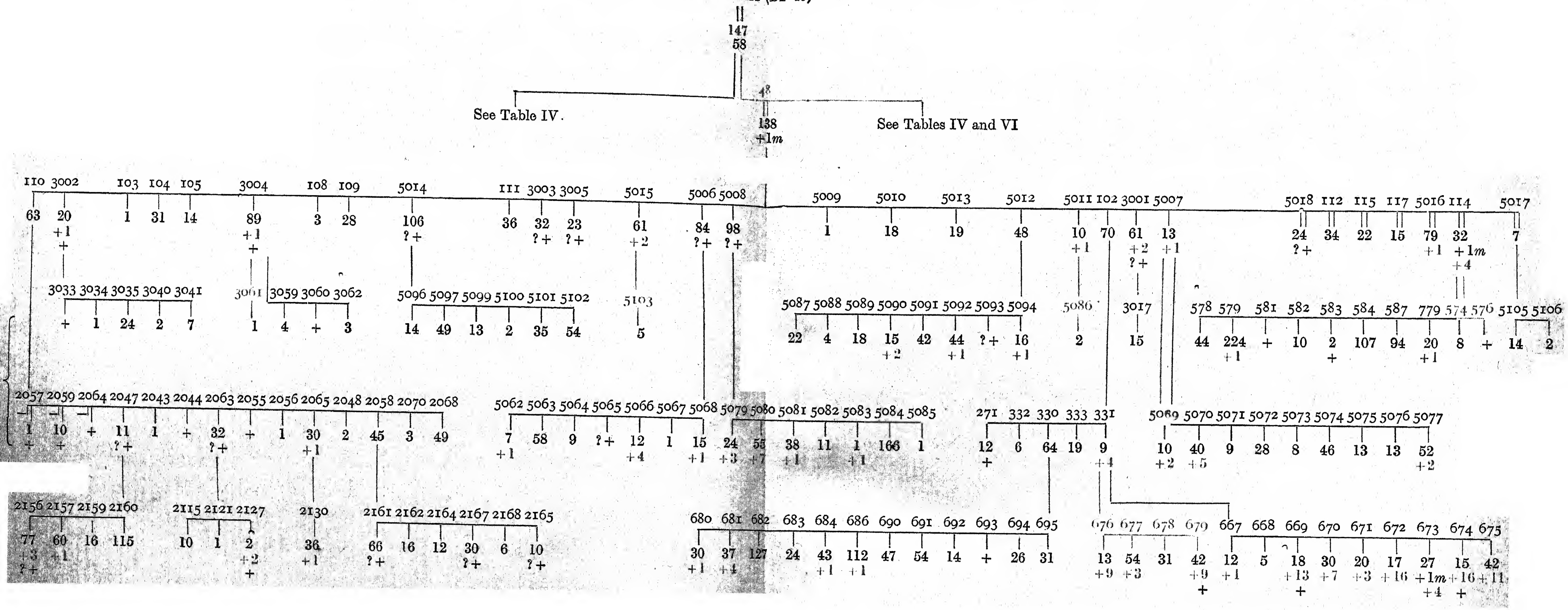
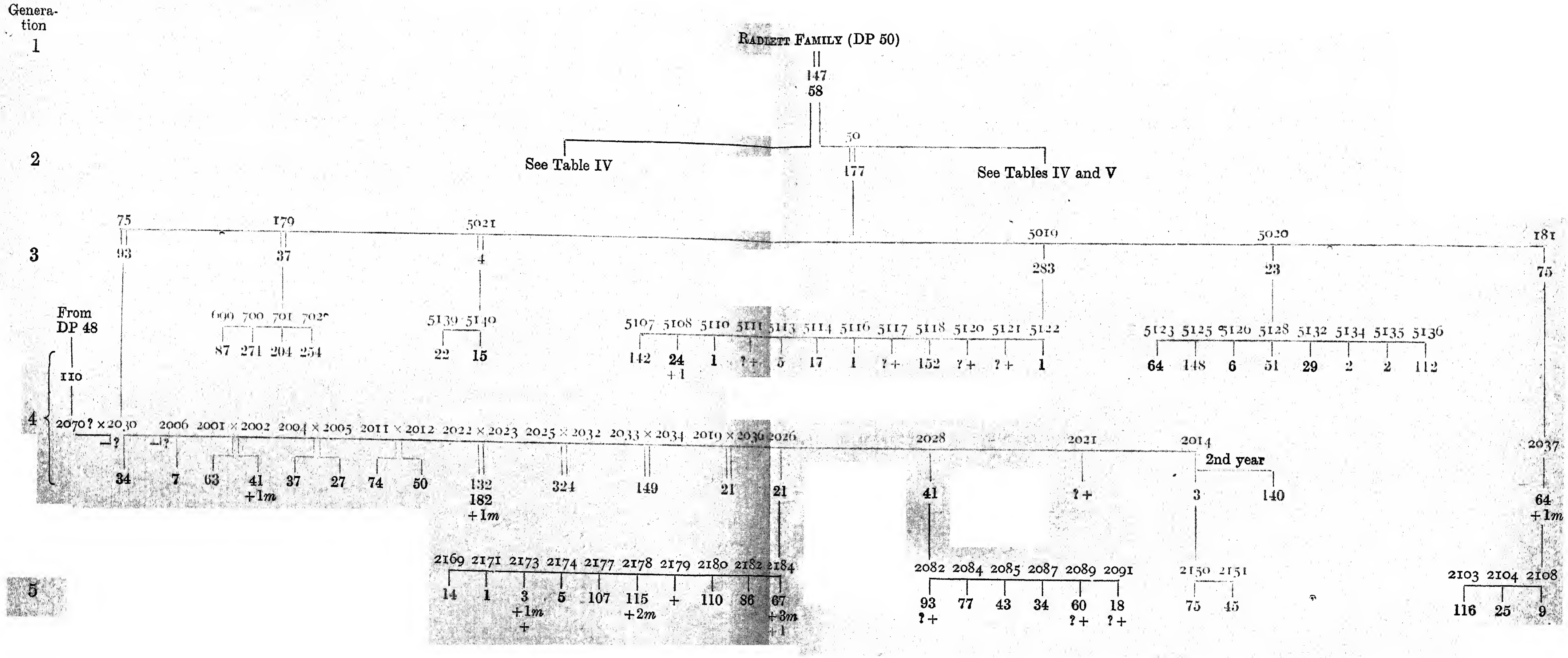


TABLE VI.


Generation
1
2
3
4
5
Radlett Family (DP 50)
147
58
See Table IV
50
177
See Tables IV and V
75
93
179
37
5021
4
5010
283
5020
23
181
75
From DP 48
110
699 700 701 702
87 271 204 254
5139 5140
22 15
5107 5108 5110 5111 5113 5114 5116 5117 5118 5120 5121 5122
142 24 +1 1 ?+ 5 17 1 ?+ 152 ?+ ?+ 1
5123 5125 5126 5128 5132 5134 5135 5136
64 148 6 51 29 2 2 112
2070 ? × 2030
2006
2001 × 2002
2004 × 2005
2011 × 2012
2022 × 2023
2025 × 2032
2033 × 2034
2019 × 2036
2026
2028
2021
2014
2037
34 7 63 41 +1m 37 27 74 50
132 182 +1m
324
149
21
21
41
?+
2nd year
3 140
64 +1m
2169 2171 2173 2174 2177 2178 2179 2180 2182 2184
14 1 3 +1m + 5 107 115 +2m + 110 86 67 +3m +1
2082 2084 2085 2087 2089 2091
93 ?+ 77 43 34 60 ?+ 18 ?+
2150 2151
75 45
2103 2104 2108
116 25 9

EXPERIMENTAL AND BIOMETRICAL INVESTIGATIONS ON DIMORPHIC VARIABILITY OF *FORFICULA*.

By the late D. M. DIAKONOV.

Laboratory of Genetics and Experimental Zoology at the University in Leningrad.

Preface.

The following investigation of my prematurely deceased pupil and afterwards fellow-worker at the University and Bureau of Eugenics D. M. Diakonov was finished by him a year ago and reported to the Congress of Russian Zoologists in Petrograd in December, 1922.

In May, 1923, began his grave illness (tuberculosis of the adrenal glands) which on the 30th September terminated his life at the age of 30, when he was yet full of vigour and energy. His illness prevented him from revising the translation of his work into English and finishing the drawings, which is now done by his nearest friends and colleagues.

Prof. Jur. Philiptschenko.

CONTENTS.

[In a lengthy introduction, not here reproduced, the author points out that bimodal variation, such as that seen in *Forficula*, need not be interpreted as a true genetic dimorphism. A similar distribution might result as a consequence of some special instability, the normal reaction to some unknown external influence being thus regarded as bimodal in its effects. This idea is further developed on pp. 227–30. W. B.]

I.

The present study represents an attempt to investigate the dimorphism, or, better, the dimorphic variability of the male *Forficula*. The length of the forcipes of the male not often varies widely, but may

then present a typical bimodal curve of frequency, the males separating into two distinct groups connected by rather scarce intermediate forms: one group having shorter forcipes, the other longer ones. We shall call the males belonging to the first of these types *forma brachylabia*, those belonging to the second one *forma macrolabia* (Semenov Tian-Shansky, 1910).

Unfortunately, mathematical statistics do not provide us with methods for precise computation, description and characterisation of bimodal curves. There exist methods for resolving a compound asymmetrical curve into its supposed simpler components, but it is not seldom of importance to characterise mathematically a bimodal curve as a phenomenon in its entirety. Since this study is simply an attempt to make a biological analysis of the phenomenon, I will endeavour to show on this material that it may be considered as an instance of a complicated normal reaction; that the differences between the male *Forficula* represent a modification, *i.e.* they do not depend on the genotypical composition of the individuals; and that at the same time it is impossible to point out any alternative external cause which could produce the observed dimorphism of a population.

Bateson and Brindley (1892) were the first to show that the forceps length of the male *Forficula auricularia* L. of the Farne Islands has a bimodal frequency curve and afterwards this curve as an illustration of bimodal curves has been reproduced in all works treating on variability. The authors themselves left the question of the causes of this dimorphism unsettled. Likewise in Bateson's well-known book (1894) there is emphasised only the presence of two centres of biological equilibrium, without any suggestion as to the actual causes of it.

However, various conjectures did not fail to appear in the works of some other authors always seeking some sharply limited alternative cause compelling a part of the individuals composing the population subjected to its influence to develop after a specific type.

Giard (1894) was the first to offer the supposition that the dimorphism of *Forficula* was due to parasitical castration caused by gregarines living in their intestines. He maintains that the gregarines could cause a weakening of the secondary sexual characters and that only the intestine of individuals of *brachylabia* contained parasites, or at least a greater quantity of them. Wheeler (1910) supported this opinion.

G. Smith (1905), as is well known, established that the dimorphism observed in certain Crustacea is connected with differences in the functional state of their testes and alterations produced by age; he supposed

that the dimorphism of certain male insects, also including *Forficula*, is of the same phylogenetic origin, *i.e.* based on differences in the sexual state, which in its turn depends on external causes.

Further, Semenov Tian-Shansky (1910) considers the dimorphism of the earwig to belong to the category of aberrations, which he determines as individual deviations due to accidental influences (physical, chemical and nutritive) upon the several individuals of a population.

Lastly, Lang (1915), in his summary, indicates by way of instances many ways of explaining the dimorphism of the *Forficula* male, and admitting that it may be explained as a purely modificational phenomenon, proceeds to point out the necessity of the existence of particular external causes influencing part of the population.

Thus all the authors quoted insist upon the presence of one or another influence, but always a specific alternative one to which but a part of the individuals is subjected, this being the cause by which the dimorphism of a population must be caused.

II.

My experiments with earwigs and observations on them were made at the Biological Station of the University at Perm (Nijnaïa Kuria near Perm) and partly in the Zoological Laboratory of the same University in 1920 and 1921; the material for preservation was collected there too in 1918 and 1922[1].

Earwigs are by no means frequent in the neighbourhood of the Station and only at one place indicated to me by the Director of the Station on two small spots in a wood, situated side by side (I call them "the left" and "the right"), there were found some colonies of *Forficula auricularia* L. The earwigs lived beneath the bark of tree stumps. But in these places the number of earwigs did not attain the enormous abundance of them on the Farne Islands (Bateson and Brindley, 1892) and the Scilly Islands (Brindley, 1914), so that my material is much scantier than that there obtained.

The above-mentioned dimorphic variability of the forceps-length of the male is not only a constant character of *Forficula auricularia* L. but may be observed also in other species of Dermaptera. Of the latter there is in my possession only some material of *Forficula tomis* Kal. and a small

[1] I express my greatest gratitude to the University of Perm, the Association of Naturalists at the same University under whose management the station is, to the Director of the Station, Prof. D. M. Fedotov, and to Prof. W. N. Beklemishev who kindly collected earwigs for me in 1922.

casual collection of *Labidura riparia*, but to systematists it is well known that many representatives of Dermaptera are dimorphic in the size and shape of the forcipes of the male and that in some species the difference between both forms (*macrolabia* and *brachylabia*) is still more marked than in the common earwig.

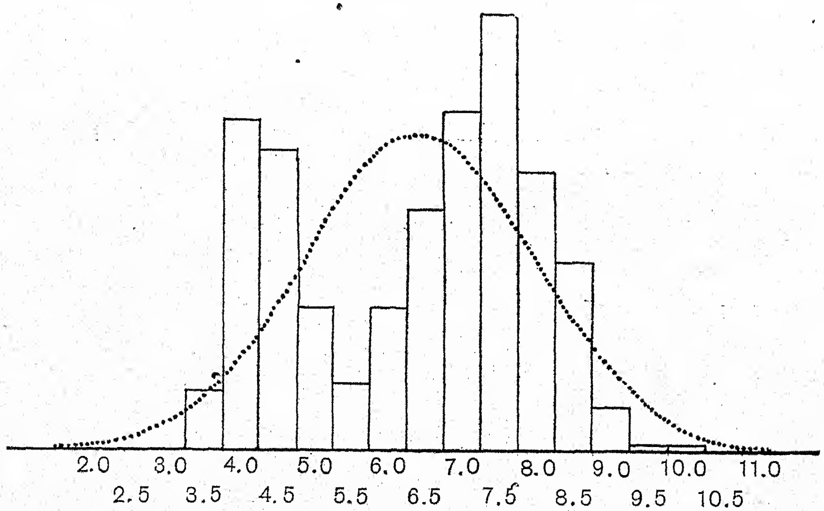
Table I gives the results of the measurements of the forceps-length of *Forficula auricularia* males from Nijnaïa Kuria (near Perm) collected during four seasons[1]. The measurement itself was carried out with accuracy

TABLE I.

The F. auricularia *L.* (*Nijnaïa Kuria*) ♂♂. *Forceps-length in millimetres.*

No. of individuals pro mille — Classes	2·0	2·5	3·0	3·5	4·0	4·5	5·0	5·5	6·0	6·5	7·0	7·5	8·0	8·5	9·0	9·5	10·0	10·5	11·0	No.*
1918	—	—	—	24	133	89	56	27	58	95	136	173	111	76	18	2	2	—	—	450
The theoretical normal curve 1918	2	6	12	23	40	61	85	108	123	127	118	99	76	52	33	18	9	4	2	
1920	—	—	—	59	363	161	52	31	39	56	99	77	51	8	3	—	—	—	—	1135
1921 *a*	—	—	—	16	286	122	38	33	57	68	114	137	89	35	5	1	—	—	—	754
1921 *b*	—	—	—	51	404	146	24	27	61	61	93	90	40	3	—	—	—	—	—	376
1922	—	—	—	20	390	140	40	70	30	90	100	90	30	—	—	—	—	—	—	100

* No. always signifies the total number of the measured specimens.



Graph of Table I, 1918.

[In all the graphs the abscissae represent the length in mm., the ordinates—the number of individuals pro mille.]

Continuous line—actual polygon, dotted line—theoretical normal curve of the forceps-length of *F. auricularia* males. Perm, N. Kuria, 1918; No. = 450 (*v.* the text, Tables I, II, III).

[1] In 1919, owing to the civil war, the work of the station was suspended and collection of material was not possible.

up to 0·5 mm.; the readings were taken from the limit between the last segments of the body and the base of the forcipes on the left-hand side. The degree of curvature of the forcipes, of course, was not taken into consideration. When the difference between the length of both forcipes was insignificant their mean size was taken and in the cases of considerable asymmetry the specimen was altogether discarded. Brindley (1914 *a*) indicates that in order to measure the forcipes they must be torn off, but I think that my method is quite satisfactory, as the accuracy was within 0·5 mm.

The graphs for these series may be found from the separate Tables I, II and III. We see that in all the collections the bimodal character of variability is maintained but that the configuration of the polygon changes: in 1918 the right-hand side prevailed (*macrolabia*), in 1920 the left-hand side (*brachylabia*); in 1921 it varies[1]. In the collections after 1918 we are struck by the enormous percentage of specimens in the first modal class, which is invariably formed by specimens with a forceps-length of 4 mm. The second empirical mode lies in the classes of 7 or 7·5 mm. The range of variation of the right side is always wider than that of the left one, which is observed also in the material from the Farne Islands (Bateson and Brindley, 1892).

Table II gives the chief constants, computed for the series on Table I. It has been already mentioned that we have no adequate methods for characterising such complicated frequency curves as the bimodal, as the proposed ones represent either a dissection into components or a rough description of each separate part of the empirical series. Neither of them gives the necessary characteristic of the entire series as a whole. Therefore in Table II are given only the usual constants for simple series, which, however, representing the functions of moments of the first four powers, may, with certain reserves, serve to characterise also more complicated instances. In the table are given: the arithmetical mean of the whole series (M), the standard deviation (σ); the coefficient of variability, *i.e.* σ expressed in percentages of M (C); the skewness $\left(Sk = \frac{\mu_3}{\sqrt{\mu_2^3}}\right)$ and the excess $\left(Ex = \frac{\mu_4}{\mu_2^2} - 3\right)$. When errors are cited they always signify the standard error. The moments of even power are always calculated with Sheppard's corrections.

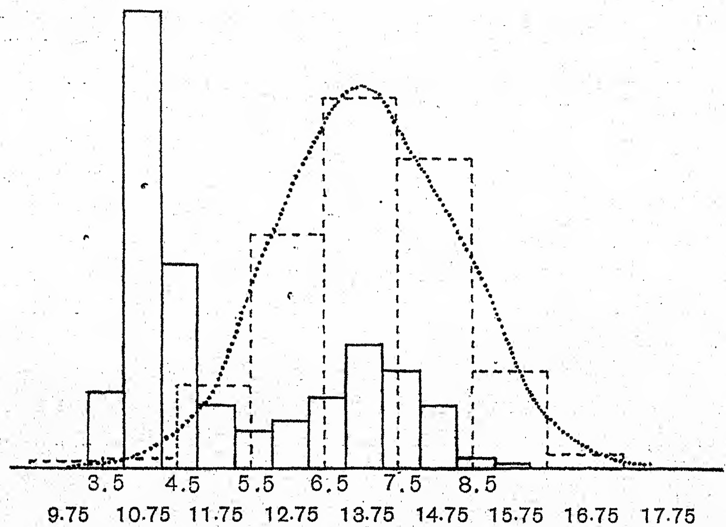
A very striking feature is the great variability of the series, *i.e.* the considerable value of σ in comparison with M, so that the coefficient of

[1] For explanation of the difference between the two collections of 1921 see section III.

TABLE II.

The chief constants for the forceps-length of F. auricularia ♂♂ (*N. Kuria*).
(*See also Table I.*)

	$M \pm m$ mm.	σ mm.	C %	Sk	Ex	No.
1918	6·399±0·074	1·569	24·51	−0·333	−1·173	450
1920	5·186±0·043	1·459	28·12	+0·747	−0·982	1135
1921 *a*	5·789±0·058	1·603	27·69	+0·177	−1·543	754
1921 *b*	5·154±0·074	1·430	27·74	+0·701	−1·127	376
1922	4·950±0·138	1·379	27·86	—	—	100



Graph of Table I, 1920 and of Table VIII.

Continuous line—actual polygon of the forceps-length of *F. auricularia* males. Perm, N. Kuria, 1920; No. = 1135 (*v.* the text, Tables I, II, III). Interrupted line—actual polygon, dotted line—theoretical normal curve of the body-length of *F. auricularia* males. Perm, N. Kuria, 1918; No. = 450 (*v.* the text, Table VIII).

variability is equal to 24–28 per cent., and then everywhere the rather considerable negative excess, resulting from the bimodality of the series, though the quantity of the excess is influenced and to a degree even obscured by the asymmetry of the series, which can be easily remarked in the tables.

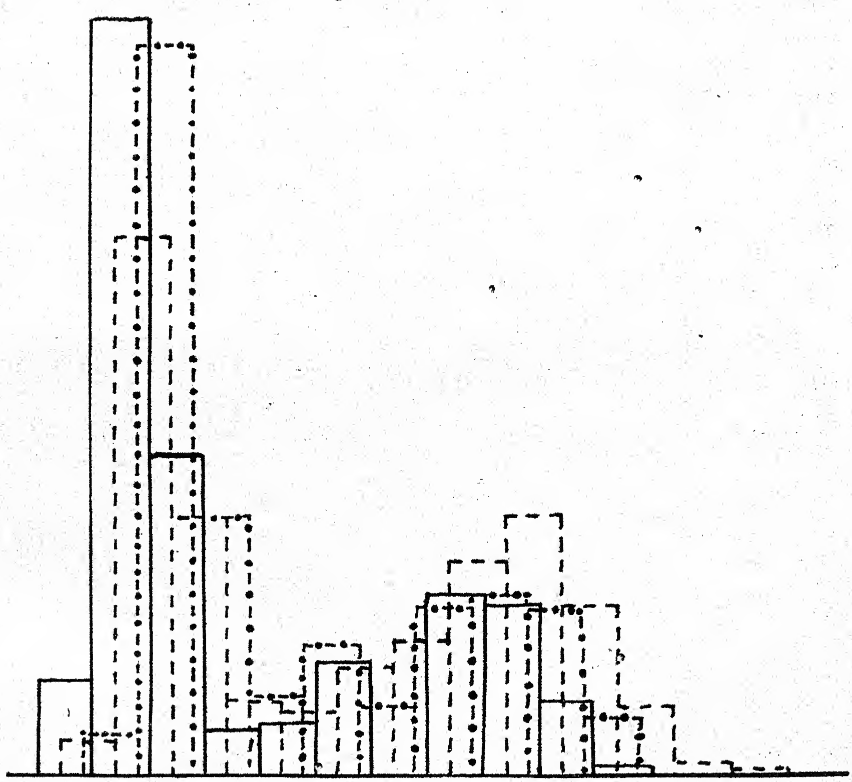
On a separate table (I) we have drawn the normal curve basing its calculation on σ (*i.e.* μ_2) of the empirical distribution. Here, too, from Table I it will be seen that the range of the empirical distribution is much less than that of the theoretical normal curve, which is characteristic of the negative excess.

TABLE III.

F. auricularia ♂♂ (*Nijnaïa Kuria*).

	Brachy-labia %	*Macro-labia* %	±*m* %	No.	Breadth of pronotum in mm.* $M \pm m$	No.	Length of the body in mm.* $M \pm m$	No.
1918	30·2	69·8	2·2	450	2·0882±0·0058	433	13·843±0·053	450
1920	63·7	36·3	1·4	1135	2·0052±0·0085	212	13·878±0·052	435
1921 *a*	46·1	53·9	1·8	754	2·0127±0·0059	462	14·588±0·043	670
1921 *b*	62·5	37·5	2·5	376	1·9546±0·0084	219	13·457±0·057	352
1922	59·0	41·0	4·9	100	1·9786±0·0116	88	13·599±0·134	91

* For explanation see the text below.



Graph of Table I, 1921–2.

Actual polygons of the forceps-length of *F. auricularia* males. Perm, N. Kuria. Interrupted line—1921 *a* (from under the bark of stumps); No.=754 (*v.* the text, Tables I, II, III, XIX). Continuous line—1921 *b* (from the fibre); No.=376 (*v.* the text, Tables I, II, III, XIX). Interrupted line with dots—1922 (from the fibre); No.=100 (*v.* the text, Tables I, II, III).

It has been already pointed out how important it is to characterise the series as a whole, but in one respect the comparison of both parts

of the bimodal curve has proved very useful: that is, the comparison of the area, *i.e.* the relative number of individuals of *brachylabia* and *macrolabia*. Such a division is, of course, artificial but not quite arbitrary for the natural limit is formed by a class consisting of the least number of individuals and this minimum proves to be a rather constant one; in our division into classes it falls on the values of 5 or 5·5 mm. This stands in connection with the modi being rather constant too. I made it a rule to consider the classes up to 5 mm. inclusively as *brachylabia* and those beginning with 5 mm. upwards as *macrolabia*; such a division coincides with the general impression of the habitus. In the first columns of Table III are given the total numbers of both forms in percentage and their standard error. No. always signifies the total number of the measured specimens.

Thus we see that the relative number of specimens of both forms in a population varies on different occasions and although the conversion of graduated variates into alternative dimorphism cannot be considered otherwise than an artificial method, this nevertheless very impressively characterises a population and may be, as we shall see later on, successfully applied in the investigation of certain particular questions.

This complex variability occurs only in the forcipes of the male. The forcipes of the female vary in a much simpler way as is seen from Table IV, where there is given by way of instance one of the collections of females, whose forcipes were measured with an ocular micrometer[1].

TABLE IV.

The length of forceps of F. auricularia ♀♀ (*N. Kuria*, 1921).

The numbers of the classes ...	1	2	3	4	5	6	7	8	9	10	11	No.
Empirical distribution ...	2	6	10	21	29	45	39	24	16	5	3	200
Theoretical normal distribution	1	4	11	22	34	40	37	27	15	6	2	200

The total range: from 3·175 mm.—4·275 mm. The class range = 0·11 mm.
$M = 3{\cdot}744 \pm 0{\cdot}015$ mm. $\sigma = 0{\cdot}215$ mm. $C = 5{\cdot}73$ %. $Sk = -0{\cdot}103$. $Ex = -0{\cdot}085$.

Here we see that the variability is inconsiderable, that the skewness and excess are practically equal to zero and that the character varies according to the normal curve.

Of the other species of *Forficula* I can produce only a small collection of *Forficula tomis*, which I made near Saratov (on the farm Opakov, in the ground of an orchard) in June, 1920. *F. tomis* is a species considerably

[1] The measurements as well as the calculations of the constants were originally made with an ocular micrometer and only after this all the necessary values were converted into mm. including the class-range, which was equal to one division of the micrometer.

larger than *F. auricularia* and differs from it also in the shape of the forceps of the male, but here, too, the same dimorphism in size occurs. In my collection there were only 109 males, which gave the distribution in forceps-length shewn in Table V.

TABLE V

Classes in mm.	4·5	5	5·5	6	6·5	7	7·5	8	8·5	9	9·5	10	10·5	11	11·5	No.
Number of individuals %	3	6	14	9	6	3	4	4	6	12	11	10	9	3	1	109

Brachylabia 37·6 %; *macrolabia* 62·4 %; $M = 7{\cdot}931 \pm 0{\cdot}190$ mm.; $\sigma = 1{\cdot}984$ mm.; $C = 25{\cdot}01$ %.

So we find in *F. tomis* the same great variability and two distinct modes as in *F. auricularia* ♂. The forcipes of the females, like those of *F. auricularia*, did not show anything particular.

Besides *F. tomis* I have a few specimens (50 ♂ and ♀) of *Labidura riparia*, collected by Prof. W. N. Beklemishev on the shore of the Aral Sea (Station on the Samara-Tashkent railway, Bolshoi Sary Cheganak Bay) in August of 1921. Their number is too small to allow of a precise calculation, but still it is worth while to give their measurements.

TABLE VI.

The length of Labidura riparia *forcipes in millimetres.*

Classes in mm.	5	5·5	6	6·5	7	7·5	8	8·5	9	9·5	n
♂	—	—	4	6	3	3	2	4	3	2	27
♀	5	14	4	—	—	—	—	—	—	—	23

The difference between the males and females here too is obvious. Apparently the forceps-length of the *L. riparia* ♂ possesses the same dimorphism as the representatives of the genus *Forficula*.

Until now I have given the absolute measure in millimetres of the forceps-length. These values could be expressed also in their percentage relation to the length of the body of the individual. In the following table I give such a series, though this method of representing is much less characteristic and should not be employed altogether considering the inexactness of the measurement of the length of the body.

TABLE VII.

The forceps-length of F. auricularia (*N. Kuria*, 1918) *in percentage of the body-length.*

Classes in %	26–29	30–33	34–37	38–41	42–45	46–49	50–53	54–57	58–61	62–65	66–69	No.
No. of individuals pro mille	11	131	102	71	87	127	167	144	96	40	11	450

$M = 47{\cdot}002 \pm 0{\cdot}477$; $\sigma = 10{\cdot}110$; $C = 21{\cdot}51$ %; $Sk = -0{\cdot}162$; $Ex = -1{\cdot}083$.

Even in such a series all the characteristics of the forcipes of the males are repeated: bimodality, negative excess and great variability.

The measurement of the body-length could be of essential importance in another respect; namely to establish whether the male of the earwig is dimorphic in any other characters besides the forcipes, and in the first place in its general size. Unfortunately, the length of the abdomen does not allow of exact measurement, since its segments are capable of telescoping. Therefore, it is necessary to find some other dimension which could independently serve as a measure of the individual. For this purpose I have taken the breadth of the pronotum measured with an ocular micrometer. But, with certain reserves, I have also availed myself of the length of the body without the forcipes. Using a collection measured at the same time it is admissible to avail oneself with some assurance of the body-length, if they are measured in a fresh condition or preserved in such a state. Old spirit collections must not be used for comparison. It is with such reserves that I have employed this method of measuring, because with fresh material the extension or compression of the abdomen is of no great consequence after all.

In the two following tables are given, for instance, the distributions of one of my collections according to the body-length measured from the anterior edge of the labrum to the point of attachment of the forcipes (at the sides) and the maximal breadth of the pronotum (at its top).

TABLE VIII.

The length of the body of F. auricularia ♂♂ (*N. Kuria*, 1918) *from the anterior edge of the labrum to the point of attachment of the forcipes* (*at the sides*).

Classes in mm.	9·75	10·75	11·75	12·75	13·75	14·75	15·75	16·75	17·75	No.
Empirical series	2	3	34	93	147	127	39	5	—	450
Theoretical nor. ser.	—	4	31	99	154	114	40	7	1	450

$M = 13{\cdot}843 \pm 0{\cdot}053$ mm.; $\sigma = 1{\cdot}130$ mm.; $C = 8{\cdot}15\ \%$; $Sk = -0{\cdot}160$; $Ex = +0{\cdot}143$.

TABLE IX.

Maximal breadth of the pronotum of F. auricularia ♂♂ (*at the top*).

The numbers of the classes	1	2	3	4	5	6	7	8	No.
Empirical series	—	7	46	96	147	102	30	5	433
Theoretical normal series	1	8	41	106	142	96	33	6	433

The total range: from 1·6918 mm.—2·3988 mm. The class range $= 0{\cdot}1010$ mm.
$M = 2{\cdot}0882 \pm 0{\cdot}0058$ mm.; $\sigma = 0{\cdot}1196$ mm.; $C = 5{\cdot}73\ \%$; $Sk = 0{\cdot}074$; $Ex = -0{\cdot}243$.

These characteristics, therefore, do not show any dimorphism and give a normal curve within the limits of insignificant deviations. So the general size of the earwig is quite monomorphic, dimorphism being a

specific characteristic of the forcipes of the males. If we admit the variability of the forcipes to represent a modification depending on the same causes as the variability of the body, there must appear a certain correlation between these two characteristics, notwithstanding the different character of the variations. It can be determined quantitatively in two ways: firstly, by calculating the coefficient of correlation according to Bravais' formula, and secondly by comparing the average size of individuals of *brachylabia* and *macrolabia*. I have made the calculation of the coefficient of correlation only for the whole length of the body measured by a ruler. The comparison of the breadth of the pronotum is made by the second method only.

TABLE X.

Correlation of forceps-length and body-length of F. auricularia ♂♂ (*N. Kuria*).

1918	$r=0{\cdot}583\pm0{\cdot}031$	No. = 450
1921	$r=0{\cdot}641\pm0{\cdot}031$	No. = 370

TABLE XI.

Comparison of the size of individuals of brachylabia *and* macrolabia *of* F. auricularia ♂♂ (*N. Kuria*).

		Brachylabia		*Macrolabia*		
		$M_{br}\pm m_{br}$	No.	$M_m\pm m_m$	No.	$(M_m-M_{br})\pm m$
Length of body in mm.	1918	12·964±0·093	136	14·225±0·054	314	1·261±0·107
	1921	13·967±0·066	180	15·124±0·074	190	1·157±0·099
Breadth of pronotum in mm.	1918	1·926±0·0068	98	2·133±0·0057	300	0·157±0·0108
	1921	1·926±0·0068	127	2·093±0·0076	181	0·167±0·0102

Both tables obviously show that the supposed correlation really exists, *i.e.* that the individual *macrolabia* is on the average perceptibly bigger than the individual *brachylabia*. This is made evident also by the measurements of the body-length and the parts of the chitin integument such as the breadth of the pronotum. On the last table the difference exceeds its standard error by 11–16 times, *i.e.* it is always absolutely real.

If such a correlation exists, it may be supposed *a priori* that the relative number of both forms in a population will change parallel with the mean size of the individuals or any other measures taken of the chitin integument. In Table III are given the mean length of the body and the mean breadth of the pronotum for all the collections together with the relative numbers of both forms among them. The breadth of the pronotum everywhere varies in proportion to the relative number of *macrolabia* males. As to the body-lengths, a comparison of them cannot

be recommended, if they belong to collections of different years, as already mentioned; the collection of 1918, in particular, had been measured in a condition of fresh preservation (that is why it was chosen for representing the variability of this character), the other collections have been kept for some time in spirits. But even if we leave out of consideration the collection of 1918, it still can be observed that as long as the number of individuals of *macrolabia* amounts to 40 per cent. the mean size of the body is less than 13 mm., and that when it rises to 54 per cent. the mean size of the body too rises above 14·5 per cent.

Thus we see, especially as the breadth of the pronotum is quite sufficient for characterising the size of an individual, that the same conditions under which the mean size of the individual increases lead to an increase of the relative number of individuals of *macrolabia* as *e.g.* in diverse years owing, probably, to variation in the climate or different conditions of life as in the two collections of 1921 (of which more will be said further on). This is a fact of great importance, because it indicates the possibility that the relative number of individuals of both forms may be a character which is modified by the same small differences in external conditions as the mean size of the individuals.

Besides the pronotum the breadth of the last abdominal segment was also measured at the upper part in the point of attachment of the forcipes and between the ends of two outstanding pointed knobs. In connection with the strong development of the forcipes this part of the abdomen of the male differs considerably in its structure from that of the female and this character might perhaps be expected to vary like the forcipes themselves. However, their curve of distribution is unimodal, as the following table shows.

TABLE XII.

The maximal breadth of the last abdominal segment of F. auricularia ♂♂ (*N. Kuria*, 1918).

The numbers of the classes	1	2	3	4	5	6	7	8	9	10	No.
Empirical distribution	10	10	37	73	108	135	67	17	1	—	458
Theoretical normal distribution	2	13	41	87	119	106	61	23	5	1	458

The total range: from 2·58–3·81 mm.; the class range $=0·154$ mm.
$M=3·228\pm0·011$ mm.; $\sigma=0·229$ mm.; $C=7·09$ %; $Ex=+0·222$.

Thus here we find neither bimodality nor negative excess. However, we observe some greater connection between the length of the forcipes and the breadth of the last segment, than between the other characters as a comparison of the following coefficients of correlation will show.

TABLE XIII.

Coefficients of correlation of F. auricularia ♂♂ (*N. Kuria*, 1921).

r (forceps-length and length of the posterior segment)	$=0{\cdot}749 \pm 0{\cdot}023$	No. $=370$
r (forceps-length and body-length)	$=0{\cdot}641 \pm 0{\cdot}031$	
r (body-length and breadth of posterior segment)	$=0{\cdot}651 \pm 0{\cdot}031$	

So the correlation coefficient of the length of the forcipes and the breadth of the last segment is even greater than the correlation coefficient of this latter and the general length of the body.

Having ascertained that the individual *macrolabia* is on the average bigger than the individual *brachylabia*, we have left quite out of consideration the question whether there exists any morphological difference between these two forms besides the forcipes which are well known to be different not only in size but also in form: in *macrolabia* they are of oval shape, in *brachylabia* more roundish, though among them there occur oval ones. Unfortunately, these differences do not admit of an exact quantitative computation.

There is no doubt whatever that it is impossible to the unassisted eye to discover any easily discernible differences between the forms of *brachylabia* and *macrolabia*. Systematists are also well aware of this fact. But we may always expect to find more elusive differences usually of a transgressive kind in proportions, *i.e.* in the relative dimensions of different parts of the chitinous tegument (skeleton).

In order to elucidate this I have measured the dimensions of several parts of the chitinous skeleton of a small number of individuals belonging to both forms (*i.e. macrolabia* and *brachylabia*) and both species at my disposal—*F. auricularia* and *F. tomis*. Out of these measurements there were composed the most rational relations or indices which it was possible to compare. On the body itself (and the wings) were measured the following thirteen dimensions: the breadth of the elytra put in relation to their length; the squama of the wing in relation to the length of the elytra (absent in *F. tomis* as a wingless form); the breadth of the pronotum in relation to its length; the length of the medium suture of the head in relation to the width of the head behind the eyes; the breadth of the third segment in the narrowest part to its length; the breadth of the first sternite in its posterior part to its length; the breadth of the submentum to its length.

Not only however has the comparison of all these indices of both forms yielded a negative result, but the indices proved to be identical for both forms of *Forficula*, *i.e.* to constitute generic characters. Still less we can expect them to serve as distinctions between forms within

the limits of species. Therefore it is not worth while to give the respective figures.

Somewhat different results have been obtained by comparing the relative length of the separate joints of the antennae and tarsus. Here there has been measured the length of all the first five joints of the right antenna and the length of all three joints of the right hind foot. The antenna was measured at the inner border, the tarsus at the outward or back side, the front edge turned upwards; its second joint was measured from the outer border of the base to the rim of the oval lobes and the third to the base of the claws. In the systematics of Dermaptera the antennae and legs are used for the determination of species and, in fact, the relation of each of the joints measured in the antenna to the sum of all five of them, and likewise of each of the three joints of the tarsus to their sum. These relations in both species of *Forficula, i.e. F. auricularia* and *F. tomis* have proved to be absolutely different and in certain relations this difference stands out very conspicuously. On the contrary, within the limits of each of the investigated species absolutely all the indicated relations in every possible combination were identical for both forms, *i.e.* the quantities remained the same for *macrolabia* as well as *brachylabia*. In the following table we give a summary of the chief results, taking for the sake of clearer demonstration the relations between two of the most distant species. Only 20 specimens of each form were measured, but even this inconsiderable number sufficed for obtaining results that leave no room for any doubt. For this table there were measured under the microscope 80 specimens, 8 dimensions on each of them.

As we have already mentioned, all other combinations of the measured parts of each of these two species of *Forficula* will give the same results, namely an entire absence of differences between the forms *macrolabia* and *brachylabia* as the respective differences either do not exceed their mean error or exceed it no more than twofold. On the contrary, the difference of the two species of *Forficula* in all these characters is quite real, as the differences are from eight to fifteen times greater than their mean error. Moreover, these tables confirm that the antennae and tarsi of *macrolabia* are on the average bigger than those of *brachylabia*, as well as the pronotum and the general length of the body, as mentioned before.

It is of course impossible to exhaust all characters admitting of a quantitative computation, but I think that the foregoing considerations will justify the conclusion that besides the forcipes it is impossible to indicate any other external morphological differences.

TABLE XIV.

Comparison of forms of macrolabia *and* brachylabia *according to relative length of the joints of antennae and tarsi.*
F. auricularia (*N. Kuria*, 1918) and F. tomis (*Saratov*, 1920).

	F. auricularia					*F. tomis*					Difference between *F. tomis* and *F. auricularia*	
	macrolabia		*brachylabia*		Difference	*macrolabia*		*brachylabia*		Difference	*brachyl.*	*macrol.*
	limits	$M_m \pm m$	lim.	$M_{br} \pm m$	$M_m - M_{br} \pm m$	lim.	$M_m \pm m$	lim.	$M_{br} \pm m$	$M_m - M_{br} \pm m$	$M_t - M_a \pm m$	$M_t - M_a \pm m$
Relation of joints of antennae in %:												
1. 4th to 1st	38–50	43·35 ±0·68	38–51	44·00 ±0·90	0·65 ±1·13	58–77	63·95 ±1·03	57–74	63·75 ±1·01	0·20 ±1·44	19·75 ±1·36	20·60 ±1·24
2. 2nd to 5th	36–50	42·1 ±0·87	30–52	43·5 ±1·42	1·40 ±1·67	22–31	26·20 ±0·42	22–33	26·40 ±0·58	0·20 ±0·72	17·10 ±1·53	15·90 ±0·97
3. 4th to 3rd	65–87	74·45 ±1·05	65–86	76·3 ±1·05	1·85 ±1·48	92–111	101·15 ±0·94	87–115	98·15 ±1·32	3·00 ±1·62	21·85 ±1·68	26·70 ±1·41
4. Absolute total length of all 5 of the antennae in mm.	—	2·165 ±0·0195	—	1·884 ±0·0181	0·281 ±0·027	—	—	—	—	—	—	—
5. Relation of the 2nd of the tarsi to 1st in %	41–58	50·00 ±0·74	43–57	50·95 ±0·84	0·95 ±1·12	47–66	59·85 ±0·99	53–75	62·10 ±1·20	2·25 ±1·55	11·15 ±1·46	9·85 ±1·23
6. Absolute total length of all three of the tarsi in mm.	—	2·485 ±0·023	—	2·177 ±0·027	0·308 ±0·035	—	—	—	—	—	—	—

So the whole statistical investigation of the variability of *F. auricularia* and *F. tomis* leads up to the following results:

The bimodal type of variability is peculiar only to the size of the forcipes of the males being a distinctive character of them. The variability of the other parts of the chitinous skeleton as well as the general length of the body is monomorphous. The relative number of individuals of the forms *macrolabia* and *brachylabia* may vary considerably, but it does so in connection with the median size of the individuals of a population, as the individual *macrolabia* is on the average in all its parts larger than the individual *brachylabia*. No other morphological differences between these two forms are found.

These results do not prove anything by themselves, but nevertheless they give some support to the supposition that the marked difference in the size of the forcipes represents a modification of the same kind as the variations in the general number of individuals, but follow according to their nature a more complex type of variability.

Further confirmation of these assumptions we will find in the results of biological experiments and observations.

III.

We required of the experiments and observations made with *Forficula auricularia* in conformity with the purport of our entire investigation the following: it was necessary to elucidate whether the forms of *macrolabia* and *brachylabia* are forms differing from each other genetically and are, consequently, hereditary, or whether they are, on the contrary, modifications, *i.e.* phenotypical results of external influences, including nutrition. And, further, should the second assumption prove more probable, is it possible to show some cause of modification exercising its action only on a part of the individuals and producing the dimorphism of the population?

Of chief importance there must be recognised the experiment of breeding. I am sorry to say that this experiment can by no means be considered successful. The earwig, to be sure, gets on very well in captivity and copulation takes place with great facility even between different species, so that females of *F. auricularia* can be mated with males of *F. tomis* without difficulty. The females fertilised by the males of their own species deposit their eggs in autumn and in winter. Under laboratory conditions the larvae hatch out and their development is completed towards spring.

The bringing up of the larvae is a good deal more difficult than keeping the adult earwigs. Besides, we had to contend with purely technical difficulties[1]. I had to give up the experiments of a whole year before having concluded them, owing to extraneous circumstances and in the following year (1921) I succeeded in obtaining as a result of all my experiments, the total of 64 specimens, only 28 of which were males. All these males belonged to *brachylabia*. According to the length of their forcipes there were 9 specimens with forcipes of 4 mm., 17 of 4·5 mm. and 2 of 5 mm. As to the parental forms, the females were always chosen among the virgin ones bred up in the laboratory; but with regard to the character under investigation the females are always indifferent, because in them no dimorphism whatever is observed. We, of course, chose males with a different forceps-length and in regard to the filial generation of the 28 males obtained at the end of our experiments the males of the parental generation were distributed as follows: the fathers of 20 of the former were typical *macrolabia* (forcipes 7·5–9 mm.), those of 6 of them belonged to the median type (forcipes about 6 mm.) and only the fathers of 2, just the biggest ones of F_1, had forcipes of 5 mm.

So the male parents of the majority of the breed were *macrolabia*, but their progeny turned out *brachylabia*.

These results are, indeed, very scanty, but nevertheless they seem to me to admit of the following explanation: under the artificial unfavourable conditions of the laboratory among the forcipes there prevails the tendency to develop only the short type, *i.e.* all *brachylabia* represent a regressive modification.

The failure of the artificial breeding may, however, be compensated in some degree by the results of the other experiments and observations related hereafter and permitting of indirect conclusions regarding this same question.

As has been already pointed out, there has been expressed in literature the supposition (Giard, 1894), supported later on (Wheeler, 1910), that the form of *brachylabia* results from partial castration by gregarines living parasitically in the intestines of the earwig.

In order to test this opinion I tried to investigate everything concerning the parasites of the earwig, and then made experiments with artificial castration of male larvae.

Gregarines (apparently *Clepsidrina ovata*) very often occur in the middle intestine of the earwig, and the dissection of 50 specimens of male earwigs of one collection proved sufficiently that the supposition of

[1] In the first place the very low temperature in the laboratory, owing to the lack of fuel.

Giard has no foundation whatever. Along with the dissections the length of the forcipes was measured and the quantity of gregarines estimated on inspection. Moreover, in the registers of dissections the condition of the testes was noted. In Table XV the results of the dissections of the earwigs are distributed according to the length of the forcipes as usual only into two groups. Beside the actual number the greatest number of individuals to be expected if the length of the forcipes is assumed to be quite independent of the presence of gregarines is indicated in parenthesis.

TABLE XV.

The length of the forcipes of the male earwigs F. auricularia (*N. Kuria*, 1921) *and the presence in their intestine of gregarines* Clepsidrina ovata.

Number of gregarines	None	Few	Mean	Many	
Macrolabia	6 (6·5)	9 (10·5)	4 (3)	6 (5)	=25
Brachylabia	7 (6·5)	12 (10·5)	2 (3)	4 (5)	=25
Number of individuals	13	21	6	10	50

The deviations from the most probable values of independent distribution are insignificant. The greatest of them is $\pm 1{\cdot}5$; moreover, they change in direction the opposite of that to be expected from Giard's suggestion. So in this instance the categorical conclusion may be drawn that no connection whatever exists between the forceps-length of the earwig males and the presence, absence or number of gregarines in their intestine.

Only when all my experiments were already concluded I got acquainted with the work of Brindley (1918) who had, as it proved, made a similar investigation and come to the identical result. Out of his 23 *brachylabia* males 12 were infected, 11 uninfected, and of 23 *macrolabia* 11 were infected and 12 were not.

So the gregarines must be eliminated from the causes of dimorphism. Yet these dissections have shown to me that these gregarines, as intestinal gregarines in general, do not influence the condition of the testes, for in the most infected specimens one could see fully-developed sound testes filled with spermatozoa. Under-developed or prematurely degenerated testes occur from time to time but without any connection either with gregarine-infection or with forceps-length.

In order to obtain certainty as to the rôle of the testes in the development of the one or the other form of the forcipes I have made experiments in artificial castration.

For the purpose there were extirpated both testes in the larvae of males, chiefly of those being in the penultimal instar, *i.e.* those that had

to pass through two more moults. The operation of the larvae was made under a narcosis of ether sulphuricum and the wound pasted up with melted paraffin. When the operation is made with sufficient care the animal sustains it rather well, but the death-rate was very great at the first moulting, when the epidermis adhering to the wound in a somewhat abnormal manner could not be thrown off, causing the death of the animal.

We obtained only five perfect castrates in which the absence of the testes was later on verified at their dissection. Four of them belonged to *brachylabia*, and five had forcipes 6·5 mm. long, *i.e.* they belonged to *macrolabia* and resembled this type also in general appearance.

Thus we see that the total absence of testes in the first place does not interfere at imaginal moulting with the formation of the forcipes which are quite normal in the male. Secondary sexual characters develop after castration, as commonly in insects, unlike mammals and many crustacea. Moreover, and this is very important here, in *Forficula* the formation of forcipes of the long type is possible even for castrated individuals.

From my point of view the fact that matters is that castration, provided the operation is made successfully, does not exhaust the individual. It is even the reverse: the absence of testes, which do not undergo any regeneration, rather conserves in the animal the nutritive material which otherwise would be spent on the formation of spermatozoa. As a matter of fact three of my castrates, among them those with longer forcipes, proved of great vitality and lived under my observation a long time. They not only retained their morphological scondary sexual characters but were endowed with the normal instinct of males, copulating with females.

I also compared the testes in both forms. First on dissection, a look at the testes conveys the impression that there is no difference between them and those of *brachylabia*; they are always developed quite normally, containing spermatozoa as in *macrolabia*. But for detailed examination the testes of both forms were preserved and sectioned in paraffin. In the sections no difference was discernible.

As a result, it may be stated with certainty that the dimorphism has nothing to do with the condition or activity, or even with the presence or absence of testes.

Besides the gregarines at N. Kuria in the earwig there occurs another parasite of much greater importance to the investigation of the question of dimorphism than the gregarines: this is the larva of a fly *Digonichaeta setipennis* Falln., living by twos or threes at a time inside the abdomen

of the earwigs, larvae as well as adults, clinging to the inner side of the body-wall and feeding apparently on the host's adipose tissue. Reaching a very great size, it utterly exhausts the host, for after its having left the body of the earwig before pupation the latter usually perishes. This is not a case of absolute castration of the earwig, because sometimes along with the parasite the testes are found still persisting. But much more often not only the adipose tissue but the testes are totally destroyed or, more exactly, degenerated or undeveloped, as the infection apparently takes place at the younger stages.

As to the forcipes, they have in the infected individual the normal aspect, *i.e.* the development of the secondary sexual characters does not alter considerably, which, by the way, is quite natural in view of the results of artificial castration.

But it proved that almost all the infected specimens had forcipes of the short type, *i.e.* belonged to *brachylabia*. Out of 300 earwigs dissected by me for this purpose, I found only one of the infected specimens having forceps 7·5 mm. long.

In the subjoined two small tables (Tables XVI and XVII) are given the numerical results of two series of dissections expressed in form of fourfold correlation tables. In parenthesis there are given the numbers expected if the size of the forcipes were independent of the infection[1].

TABLE XVI.

The forceps-size of F. auricularia (*N. Kuria*, 1921) *and infection with larvae of* Digonichaeta setipennis *Falln. fly* (1*st series of dissections*).

	Infected	Uninfected	Totals
Brachylabia (short forcipes)	10 (6·5)	46 (49·5)	56
Macrolabia (long forcipes)	1 (4·5)	38 (34·5)	39
Totals	11	84	95

TABLE XVII.

The same as in Table XVI (2*nd series of dissections*).

	Infected	Uninfected	Totals
Brachylabia	35 (17)	71 (89)	106
Macrolabia	— (18)	109 (91)	109
Totals	35	180	215

If the first table is not quite convincing the second one (2nd series of dissections) leaves no room for doubt. The infection of the earwig with the larva of the fly determines the forceps-type of the future imago and

[1] These figures represent the result of the totals of the respective column and line, divided into the total number of cases.

the infected earwigs always prove to belong to the form of *brachylabia*. The only possible explanation of this incontestible fact appears to be this, that the parasite exhausts his host to such a degree, that at its final moulting the formation of such considerable appendages as the forcipes becomes impossible.

The single exceptional specimen with long forcipes, containing a rather big larva of the parasite cannot be considered a disproof: it might have been infected with the eggs of the fly at a comparatively advanced stage of development so that at the time of metamorphosis the parasite might have been still so small as not to exercise a great influence on the state of the host.

This observation receives some support from the following: the parasite, as has been already mentioned, previous to its pupation leaves his host, which perishes later. One collection of earwig-males was left alive for nearly a month, after which time it consisted of 124 live males (59 *brachylabia* and 65 *macrolabia*). Of 24 males remaining which died producing about 25 pupae of *Digonichaeta* all were *brachylabia*. Among the living specimens dissected one only, also a *brachylabia*, had a parasite. Thus, also, of 148 male earwigs, 44 per cent. of which were *macrolabia*, all 25 infected belonged to *brachylabia*.

If the development in infected earwigs of short forcipes only is a consequence of exhaustion and not a specific result of parasitic castration, this exhaustion should affect other characters, and these earwigs must be on the average smaller. Measuring of the body-length is here no use, as the parasite causes a considerable extension of the abdomen, altering the true length of the body. Therefore it was necessary to use the measurement of the breadth of the pronotum. Unfortunately the infected individuals of the collections of 1921 were partly picked out and dissected, so that these collections could not be made use of for this purpose. But it was possible to pick out of the remaining collections of 1920 all the apparently infected individuals (47 males) and after having measured the breadth of the pronotum to compare them with the general population of the same year. The results of this comparison are shown in Table XVIII.

Although the number of the measured infected individuals is not great, the cited difference between the mean breadth of the pronotum of both forms is seven times greater than its standard error. This proves that the infected individuals not only develop forcipes of the short type but that they are on the average smaller than the population on the whole.

TABLE XVIII.

Comparison of F. auricularia ♂♂ (*N. Kuria*, 1920) *infected with larvae of* Digonichaeta setipennis *with the population in general.*

	(*a*) General population		(*b*) Infected individuals		
	$M_a \pm m_a$	No. of measured individuals	$M_b \pm m_b$	No. of measured individuals	Difference $M_a - M_b \pm m$
Greatest breadth of pronotum in mm.	$2{\cdot}0052 \pm 0{\cdot}0085$	212	$1{\cdot}8980 \pm 0{\cdot}0129$	47	$0{\cdot}1072 \pm 0{\cdot}0154$
Length of forcipes in mm.	$5{\cdot}186 \pm 0{\cdot}043$	1135	$4{\cdot}042 \pm 0{\cdot}0295$	47	$1{\cdot}144 \pm 0{\cdot}052$
Range of variation of forcipes in mm.	3·5—9·0	—	3·5—4·5	—	

Thus we are bound to acknowledge that infection with the larva of the *Digonichaeta setipennis* fly produces by exhaustion forcipes of the short type, *i.e.* the infected *brachylabia* represent a simple modification resulting from insufficient nutrition.

As I have above indicated, the earwigs were always collected at the same place on two small spots situated side by side. So I had not, unfortunately, material from dissimilar localities for comparison. This might have been of great importance for the study of a possible modifying influence of external conditions.

It must be emphasised that it is impossible to point out any difference of conditions of the habitat of both forms. Earwigs with long forcipes and those with short ones intermingle under the bark of the same tree-stumps; Bateson (1892), too, found representatives of both groups under the same stones.

However, making my collections, I myself caused, within the limits of the two mentioned spots, an alteration in the conditions of the existence of a part of the population. As was mentioned before in collecting earwigs the bark under which they sit, usually in great numbers, had to be torn off. But they never burrow into the wood, though it is sufficiently decayed for that. After two years of collecting (1921), in one distinct section of one of the localities (the right one), the richest in earwigs the stumps were stripped of bark down to the roots. However, the earwigs did not leave these stumps, but had involuntarily changed their habits, sitting here within the dry wood instead of the bark, which was gone. As the collections were made by batches it could be observed that the earwigs from the wood differed on the average somewhat from those from under the bark, in the first place by a higher percentage of *brachylabia*.

In the tables (Tables I, II, III) the collection of 1921 is given as two separate units—*a* and *b*. The collection *a* are the earwigs from under the bark where it still remained and gathered in both localities; the collection *b* are from the wood of one place in the right-hand locality. The separate Table III represents the graph of the forceps-length of these two series, and Table XIX gives a comparison of their mean lengths.

TABLE XIX.

Comparison of two series of F. auricularia ♂♂ (*N. Kuria*, 1921) *under different conditions of existence.*

	Series *a*: from under the bark of stumps		Series *b*: from the lignin of stumps		
	$M_a \pm m_a$	No. of specimens*	$M_b \pm m_b$	No. of specimens*	Difference $M_a - M_b \pm m$
1. Relative number of specimens (*brachylabia* in %)	46·15 ±1·82	754	62·50 ±2·50	376	−16·35 ±3·09
2. Forceps-length in mm.	5·789 ±0·058	754	5·154 ±0·074	376	0·636 ±0·094
3. Body-length in mm.	14·588 ±0·043	670	13·457 ±0·057	352	1·131 ±0·071
4. Maximal length of pronotum	2·0127±0·0059	462	1·9546±0·0084	219	0·0581±0·0103

* The number measured for different characters is different, first because we had to discard defective specimens (*e.g.* for body-length), and, secondly, some characters were not measured in all the collections, but only in part, when it was possible to restrict oneself to a lesser number. Of course complete collections were never divided.

The table shows that the populations of earwigs in the wood as a matter of fact are somewhat different from those under bark. It is in all its characters on the average a little smaller and the number of *brachylabia* is greater. The difference is not great, indeed, but it would be strange to expect a considerable one from so insignificant a cause as the migration from under the bark into the wood. However, the differences of the mean sizes everywhere exceed their error by several times and these differences for all the characters taken agree in the comparative smallness of earwigs living in the wood fibre. That we have to do here not with accidental variations of numbers receives a further support from the results of a comparison of the separate independent collections, computed for each of them separately. In one of the spots (the left one) I had made three collections under the bark. In the other one (the right), one collection was also made from under the bark, and two separate collections from the wood fibre. In Table XX there are given several dimensions, characterising these separate groups, only without computation of the differences which can be easily made.

TABLE XX.

Separate collections of F. auricularia ♂♂ (*N. Kuria*, 1921).
The mean values and their standard errors.

	No. of speci-mens	Relative no. of specimens in % *Brach.*	*Macrol.*	Forceps-length in mm.	Body-length in mm.	Maximal length of pronotum in mm.
1. Left locality from under the bark	84	45	55	$5{\cdot}840 \pm 0{\cdot}183$	$(13{\cdot}043 \pm 0{\cdot}125)$	$2{\cdot}0033 \pm 0{\cdot}0128$
2. ,, ,, ,, ,,	215	49	51	$5{\cdot}707 \pm 0{\cdot}109$	$14{\cdot}714 \pm 0{\cdot}075$	$2{\cdot}0221 \pm 0{\cdot}0095$
3. ,, ,, ,, ,,	155	48	52	$5{\cdot}713 \pm 0{\cdot}113$	$14{\cdot}236 \pm 0{\cdot}083$	$2{\cdot}0072 \pm 0{\cdot}0091$
4. Right locality ,, ,,	300	43	57	$5{\cdot}882 \pm 0{\cdot}091$	$14{\cdot}863 \pm 0{\cdot}042$	—
5. ,, from the wood fibre	230	63·5	36·5	$5{\cdot}124 \pm 0{\cdot}096$	$13{\cdot}578 \pm 0{\cdot}048$	$1{\cdot}9546 \pm 0{\cdot}0084$
6. ,, ,, ,, ,,	146	61·5	38·5	$5{\cdot}202 \pm 0{\cdot}116$	$13{\cdot}221 \pm 0{\cdot}063$	—

It is clear that the first four collections approach each other very closely as well as the two last ones. The fourth collection from under the bark, though made on the right-hand spot approaches the first three more closely than the collection from the wood fibre on the same spot.

In the first four collections the percentage of *brachylabia* is less than 50, in the last two it is more than 60. The forceps-length in the first is about 5·7–5·8 mm., in the last 5·1–5·2 mm. The body-length varies in the first ones about 14·5 mm., in the last about 13·5 mm. Here we meet in the first collection with some discrepancy, but there must not be attributed to it a great importance. This is the first collection in time when the population contained older larvae, therefore it contains many young insects only just moulted with the abdomen flattened, not yet matured and even empty of food. It has been already pointed out that this character must be taken into account with great reserve. On the contrary, in the last character (the pronotum-length), forming part of the hard chitinous skeleton, the first collection does not materially differ from the following ones; while in the collection from the fibre this dimension, too, is perceptibly smaller than in the preceding ones. Unfortunately this dimension could not be established in the last collection, because it was previously used for dissection and destroyed.

So my preceding conclusion that the population in the fibre differs from that under the bark may be, as seems to me, considered proven. Most probably this is to be ascribed to a change of the conditions of existence in the fibre in comparison with those under the bark. Migrations of earwigs from stump to stump during their larval stage of life are scarcely possible, as the larvae keep in a group very close to their nest or burrow under the guard of their mother, and only the larval period can be of importance in determining the size and form. What the differ-

ence of conditions of existence may be is very difficult to tell—it may be a lesser quantity of food in the fibre, perhaps a greater dryness or something else besides. At any rate the conditions in the fibre must be considered less favourable, and the population in all its characters becomes smaller. The forcipes follow in their mean size the other characters, and, which is most important, the percentage of individuals of the left side of the curve considerably increases, *i.e. brachylabia*. The number of individuals in the modal class of this part increases nearly to one and a half. Thus the size of the forcipes is not only modified by the same factors as the general size of the body, but the relative increase of specimens of one form at the expense of the other proves to be also a modification, or, in other words, the numerical interrelation of both forms in a dimorphic population may change under the influence of altered conditions of nutrition and other external factors.

The small collection of earwigs received from Prof. Beklemishev in 1922 was again gathered from the fibre of the left locality. Although a direct comparison of collections of different years ought to be made with caution nevertheless its agreement with the collection of 1921 is obvious. The wood fibre collections of different years quite coincide as to the variation of forcipes. Unfortunately in 1922 no collection was made from under the bark. In order to determine influence of nutrition it would be necessary to make a special experiment: to divide into two groups a large population of young larvae of homogeneous origin or even better several separate families of them, and bring them up, letting one of them starve while feeding the other abundantly. I have tried such an experiment of the first kind. To my regret it entirely failed. In the abundantly fed population mould continually appeared and it perished from some semi-parasitical fungus. The cultures must evidently be kept in a drier condition. The starving population prospered better but taken alone was of small interest. It yielded no more than about twenty male imagos, all *brachylabia*, though an equal number of both forms was to be expected.

Observations on the regeneration of the forcipes were also made. The thread-like cerci of the larvae, unlike the forcipes of the adult earwig, tear off very easily, and their brittleness borders on autotomism, and they are endowed with a great capacity of regeneration. Among the free living earwigs specimens often occur with one of the forcipes as it were under-developed, recalling that of the female, so that the specimen itself looks like an external hermaphrodite. These are natural one-sided regenerants, which can be obtained also artificially if the cercus of the

larva be torn off betimes before the last moult. In general, the degree of development and the size of a regenerant are in direct proportion to the time remaining from the injury to the last moult (for particulars *v.* Diakonov, D. M., 1923). In such a case it is not the character of the regenerate which is of importance to us, but the other half of the forceps remaining after unilateral injury intact and bound to develop quite normally. It was found that all unilateral regenerants (to the bilateral ones this of course does not apply) have the intact normal forceps built after the short type, never exceeding in length 5–5·5 mm., *i.e.* all *brachylabia.*

Out of the preserved summer collections of 1921 I selected about 80 specimens of natural unilateral regenerants in which the imaginal moulting had fixed the regenerate in the most different stages of development. All belonged to *brachylabia,* while in the normal natural population *brachylabia* formed 46 per cent. (under the bark) or 62·5 per cent. (in the wood fibre)—the selected specimens could have originated under both types of conditions. As the cerci are alike in all larvae, the probability of their loss is equal for all; therefore, among the regenerants about 30 per cent. might be expected (for the wood fibre) or even 43 per cent. (for the bark) specimens of *macrolabia.* As a matter of fact there was not one among them. The artificial regenerants were not taken into account here, for, as we have seen, under artificial conditions there prevails a tendency towards short forcipes.

Thus it appears that the process of regeneration on one side of the abdomen probably absorbing too much nutritive material, or formative energy of some kind, prevents the formation of a long forceps on the other side, thus making the animal *brachylabia.*

Among insects there are known instances, though few, in which the regeneration of the appendages on one side caused a certain reduction or under-development of corresponding appendages on the other side. When the forcipes of earwigs regenerate on one side their reduction on the other side invariably attains a definite dimension—about 4–4·5 mm., which is the size of well-developed forcipes. Moreover, this dimension lies within the normal limits of the variability of the forcipes. This, too, serves as a confirmation of the *brachylabia* type being an easily obtained modification.

IV. General Conclusions.

All severe exhaustion of the larvae and unfavourable conditions as to nutrition lead to the formation of forcipes of the short type. This is observed on infection with the parasitic fly, causing general exhaustion, as well as on unilateral regeneration of the forcipes themselves resulting in local exhaustion and on rasing the larvae under conditions of starvation or under the generally unfavourable conditions of a laboratory.

But under natural conditions such severe exhaustion is a phenomenon of rare occurrence. The overwhelming majority of *brachylabia* are not subjected to such influences and under the conditions to which they are exposed it is impossible to indicate any specific cause which would lead to the development of short forcipes, as both forms are living together under the same bark.

If all specimens of *brachylabia* proved to be infected by the larvae of a fly or were regenerants, these factors would represent the specific cause of dimorphism. But this is not the case; the infected and regenerants form but a small percentage of specimens with short forcipes, but the fact that they are observed *only* among the *brachylabia* indicates that the short forcipes are of modificational and not genetic origin.

Moreover, we see that on an inconsiderable change of external conditions, for instance, a migration from under the bark of stumps into the fibre, if not an entire disappearance of *macrolabia* at least a considerable diminution of their relative number, which also confirms that the numerical relation of both forms in a population is not the result of genetical segregation, but varies under the influence of external conditions.

Thus, as concerns the male *Forficula*, we see, I think, the following: *first*, with regard to the size of the forcipes all males are genotypically homogeneous and the variations of the forcipes are pure modifications; *second*, in the natural free-living population all males, as well as the females, with exception of a small percentage of specimens infected by the fly and regenerants, exist under homogeneous conditions of life, to put it more exactly, under conditions varying accidentally, *i.e.* after the law of the normal curve.

Meanwhile the dimorphic character of the variation of the forcipes is a fact; therefore, if we consider the two previous propositions as proved we inevitably must accept this *third one*: the reaction-norm of the organism with regard to the size of the forcipes has a complex aspect: the size of the forcipes does not stand in direct relation to the conditions of development, but is particularly sensitive in the values of mean favour-

ableness and is modified more rapidly, or, and this is the same, it is more stable near two different values and varies more slowly, as has been considered in detail at the beginning of this article [not here reproduced].

In other words, the dimorphism of the *Forficula* males is due only to the complex aspect of the specific reaction-norm.

The considerations put forth in the introduction do not lose their value, quite independently of the conclusiveness of the data obtained from *Forficula*, as the former represent an *a priori* deduction, and secondly in zoological and even more in botanical literature many instances of a dimorphic reaction-norm occur, but usually the term dimorphism is applied in a very vague sense and, which is the chief point, the conception of reaction-norm in this connection has not received a sufficiently precise meaning.

The variation of the androecium in *Stellaria media* Cyr., according to the investigations of Reinöhl (1903) may serve as a wonderfully apt illustration. The number of stamens has two modi: on 3 and on 5. Under better conditions of growth, natural as well as experimental, and with increased light, the ordinate of the greater mode prevails, while the minor mode may become entirely obscured or greatly diminished. When the conditions are reversed the reverse result is observed. At the same time the position of the modi does not change, and the ordinate of the intermediate class remains in all cases of secondary significance.

The best known expressions of the dimorphic reaction-norm in botany are the so-called intermediate races ("*Zwischenrassen*"), a conception elaborated by de Vries (1901–1903). The essential in them is that the genotype in a population being apparently homogeneous, there continually appears along with normal individuals a certain number highly aberrant with some anomaly (increased number of rays of the flower or vegetative organs, supernumerary cotyledons, twisted stem, fasciation, etc.) usually connected with the normal type by comparatively rare intermediate forms.

In such a race, the degree of the anomaly itself has a certain connection with the external conditions, though Lehmann (1909) points out a greater complexity in *Veronica*. But it is impossible to enter upon the discussion of these questions here. Lastly, the classical instance of alternative dimorphism introduced by Baur is the coloration of the flowers of *Primula sinensis rubra*, which is red at the usual temperature and white under the conditions of the conservatory[1].

[1] [This reference is to the statement of Klebs to the effect that in a temperature of 30–35° C., especially in shade, the flowers are white. We have not grown "red" plants in a

In zoological literature, too, can be found instances of dimorphic reaction-norms as a constant phenomenon.

So for instance the dimorphic coloration of the caterpillars certain butterflies (Federley, 1916) proved to be in no way the result of genotypical distinctions and under apparently identical conditions the caterpillars were either dimorphic or belonging to both forms, but never to intermediate types. A similar dimorphism is observed in the coloration of the pupae of other butterflies (Lenz, 1917); here as a modifying factor there can be indicated the illumination of the caterpillars before pupation; it is of importance that the intermediate type of coloration cannot be obtained or is only found exceptionally.

As analogous to the intermediate races of plants may be considered the special race of *Cyclops* observed by Alverdes (1920). In it there appear specimens with various anomalies in the structure of certain appendages, armour, etc. The author holds that in this instance the phenomenon of genotypical segregation was not present, but that the whole race had acquired a special capacity of reacting in such a pronounced way to inconsiderable alterations in the conditions of development and environment. Something of the same kind has been observed in Daphnia (Kuttner, 1913).

Johannsen (1913) indicates that there may exist characters reacting to inconsiderable changes in external conditions. He refers chiefly to the number of rays or parts in the inflorescence of Compositae and Umbelliferae, where the critical reaction is determined by the very mechanism of development (Ludwig, 1895–1896).

At the beginning of this article the same point of view has been developed, but in a more general way: there is no need to speak of a sharp critical limit—the reaction may vary by degrees, but with a different rate. Similarly, any character may be admitted to vary in such a way if the facts suggest it, though this mechanism of development may be different and not so apparent as the formation of rays in the inflorescence of Umbelliferae.

temperature quite so high, but under ordinary stove treatment, about 27–28° C., which is much too hot for proper cultivation of *P. sinensis*, we have never seen more than a slight reduction in colour, with occasional development of whitish lines radiating from the eye. Inhibition of colour resulting in what can be called "white" may happen in some pinks, but not, I feel sure, in reds.

Professor Baur, to whom I subsequently wrote, kindly replied that for this demonstration he uses a Primula having flowers coloured approximately like the Antirrhinum figured in Pl. I, fig. 15, of his recent paper in *Bibl. Genetica*, IV. 1924, a shade which we should call pale magenta. This is quite what may be expected and there can be no further misunderstanding. W. B.]

At any rate the possibility must be remembered that dimorphism may be observed in a genotypically homogeneous population living at the same time under quite similar though of course not identical conditions of existence.

Finally, I can refer to E. Baur's well-known book (1919) in which he points to the possibility of different complex types of modifiability when the external conditions constantly vary in a definite way; only I have approached this question quite independently and in a different way, my idea being that the modifiability or, in other words, the character of the reaction-norm can be represented as a mathematical function of a different but, in each case, quite definite order and practically in the shape of a line—in the simplest case a straight line, and then, too, as a curve of different character and different order.

V. Summary.

1. The conditions of existence of any population are to be considered homogeneous only, when they vary according to the law of the normal curve.

2. There are no reasons to assume that the variation of a character must be necessarily in direct proportion to the conditions of development, in other words, the reaction-norm may represent not only a linear but a more complex kind of function of the conditions of development.

3. Therefore the form of frequency curves may be the result of the interaction between the normal variability of the external conditions and the specific behaviour of the reaction-norm. Of such an origin may be in particular also dimorphic (bimodal) variability or even the alternative dimorphism in a population genotypically homogeneous and living under quite similar conditions of development and existence.

4. Dimorphic variability is observed in the male earwigs only in the size of their forcipes and not only in *F. auricularia* but also in other species (*F. tomis*, *Labidura riparia*). The forcipes of the female vary monomorphically.

5. The body-length, breadth of pronotum and other characters vary monomorphically, but are in a certain correlation with the size of the forcipes, so that *macrolabia* are on the average in all respects a little bigger than *brachylabia*.

6. The position of both modi for the size of the forcipes varies very little, but the ordinates, *i.e.* the relative number of *macrolabia* and

brachylabia in a population, vary very greatly in different years as well as under different conditions.

7. It is impossible to indicate any morphological distinctions between the forms *macrolabia* and *brachylabia* besides the forcipes and the mean sizes.

8. On rearing under unfavourable conditions a tendency to develop forcipes only of the short type prevails.

9. The presence of Gregarines (*Clepsidrina ovata*) in the intestine has no influence on the size of the forcipes or on the state of the testes.

10. Artificial castration does not influence the size and form of the forcipes.

11. In the structure and state of the testes of both forms there is no difference.

12. The specimens infected with the parasitical larva of the *Digonichaeta setipennis* Falln. forcipes of the short type are developed which must be due to exhaustion.

13. In nature specimens of both forms occur together under the same bark, which is the normal habitat of earwigs in this region.

14. When the stumps with earwigs in one region had been deprived of their bark in subsequent years the earwigs migrated into the dry fibre of the wood. A comparison of the earwigs from these stumps showed that the relative number of *brachylabia* had greatly increased among them.

15. A unilateral regeneration of the forcipes of the males, when the larva had lost one of the forcipes, causes the other unhurt cercus to develop as in the short type.

16. As the length of the forcipes and the proportion of the two forms may be modified by a change of conditions, all variants of the forcipes of males must be considered as manifestations of the same genotype.

At the same time, for the overwhelming majority of *brachylabia* specimens, no specific factor can be named which would account for the dimorphism.

Therefore the cause of the dimorphism is only a specific and rather complex kind of reaction-norm where a modification under the ordinary conditions proceeds with particularly great rapidity.

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A NOTE ON THE INHERITANCE OF EGG-COLOUR IN THE SILKWORM

By CAROLINE PELLEW.

Student of the John Innes Horticultural Institution.

In a recent publication on "Maternal Inheritance" Uda[1] has shown that the inheritance of the egg-colours slate (normal) and brown, in *Bombyx mori*, hitherto supposed to be determined maternally, is subject to several complications. Our knowledge of the inheritance of silkworm egg-colours, before the publication of Uda's paper, had been derived from the work of the late Professor K. Toyama[2]. In this paper the reader is given clearly to understand that as regards the normal slaty and the brown colours of the eggs the inheritance is purely maternal and that batches mixed in colour do not occur[3]. But this conclusion neither agrees with Uda's statements, nor with the details given in Toyama's papers of his own breeding experiments. This ambiguity, and doubtless also the complications of the case, have led to diverse misconceptions that have now been introduced into text-books, and the object of this note is to endeavour to clear up these mistaken conclusions.

One complication, introduced both into Toyama's and Uda's experiments, is the use of divoltine and multivoltine races. In such races the eggs laid by the spring brood generally do not develop dark pigment in the serosa. Occasionally, however, some of these eggs develop pigment, and the pigmented eggs usually do not hatch till the following spring. In the investigation of egg-colour these breeds are a complication, though the fact itself may not bear on the question of the relations between different egg-colours.

Besides the slate and brown pigments, Toyama worked with blue and crimson. He states that all these pigments are deposited in the serosa, a layer produced by the fertilised embryo, whereas other egg-colours, such as whitish-grey, or yellow and white of newly-laid eggs, are due to the shell or yolk, and are purely maternal in origin. Toyama concludes that all the pigments deposited in the serosa are inherited—as is the whitish-grey—maternally, with the exception of crimson which Mendelises normally. Inspection of Toyama's tables, in which are set out the

[1] *Genetics*, VIII. 1923, p. 322. [2] *Journ. Gen.* II. 1912, p. 351.
[3] See especially *ibid.*, II. pp. 400 and 402.

details of his breeding experiments, shows that this is true in respect of the relations between slate and blue, and slate and crimson, respectively. In the slate and blue experiments no mixed broods occur, and the eggs of separate broods are all slate if the mother carries the dominant factor for slate, or all blue if she is a homozygous recessive. On the other hand, in the slate and crimson experiment, mixed broods occur, slate and crimson eggs of each mixed brood being in the ratio of 3 slate : 1 crimson; and, further, reciprocal crosses between pure forms give F_1 eggs all slate. Turning to the slate and brown experiment, we find mixed broods are recorded in considerable numbers, and these are noted by Toyama (p. 355). Moreover, these mixed broods were laid both by moths descended from brown-egg families and by moths descended from slate-egg families. These facts appear inconsistent. How Toyama proposed to reconcile the mixed broods with his representation of the inheritance is not clear. He speaks of an intended discussion of this subject, but postpones it. Unfortunately he made no crosses between pure slate and brown varieties, but worked with an impure race.

Starting with pure breeds Uda found that slate ♀ and brown ♂ gave slaty F_1 eggs, but the reciprocal cross gave brown F_1 eggs, the colour in both cases being exactly as in the pure breeds. F_2 eggs, laid by F_1 females of either type mated with F_1 males of either type, consisted of slaty and brown eggs in the ratio 3 : 1, but the brown eggs were slightly darker than those of the pure brown breed. Both the F_1 types were crossed reciprocally with slaty males and females, and gave only slaty broods. Pure brown females crossed with either F_1 type, whether slaty or brown, laid brown eggs, but the reciprocal cross, *i.e.* F_1 females of either type, fertilised by brown males, laid eggs mixed slaty and brown, in the ratio of 1 : 1.

The extensive series of experiments made by Uda leave no doubt that the facts are as described, and that we have here a peculiar combination of Mendelian inheritance and maternal influence. Two exceptions to simple Mendelian behaviour are to be observed. First, that the homozygous (recessive) brown female, however fertilised, lays typical brown eggs; and secondly, that the brown eggs in mixed broods, *i.e.* those derived from heterozygous parents, are darker than the pure brown, and apparently assume an intermediate colour between normal and brown (Uda, p. 333). Thus the somatic influence of the homozygous brown mother maintains the eggs brown, fertilisation by male cells bearing the dominant slaty factor being powerless to change this colour. But the somatic influence of the heterozygous mother is such, that though egg-

colour is mainly determined by the factorial constitution of the embryo, the brown eggs are darkened.

To sum up. The three egg-colours, blue, brown, and crimson, are all recessive to slate, and, in relation to that colour, blue is determined by the mother, crimson by the factorial constitution of the embryo, and brown by the mother when she is homozygous, but mainly by the factorial constitution of the embryo when she is heterozygous.

We have no further exact knowledge of the genetic relations between the slate, blue, brown, and crimson colours, though Toyama says that the order of dominance is probably that in which they are here set out. That a knowledge of these relations would throw light on the meaning of the facts is probable. The four egg-colours are shown in Toyama's coloured plate, and their appearance leads one to suspect that slate, blue, and brown are nearly related, and that possibly the differences may be quantitative: *i.e.* they may be multiple allelomorphs. Until further information is available, no satisfactory discussion of the facts is possible.

GERMINATION TESTS WITH POLLEN OF STOCKS.

By R. SNOW.

Department of Botany, Oxford.

The purpose of these tests was to obtain further evidence for or against the theory that in double-throwing stocks those pollen grains that carry the factor for singleness fail to effect fertilisation. As is well known, from the work of Miss Saunders (1), double-throwing stocks are heterozygous for singleness, but yet the pollen only carries the factor for doubleness. This behaviour could be understood if it could be supposed that the grains carrying singleness are formed but fail to function.

It had previously been found (2) that when counted numbers of pollen grains were put on the stigma, the ratio of the number of seeds obtained to the number of grains employed, though always very low, was yet much higher with pollen of pure single stocks than with that of double-throwers. It was also stated that "in 20 per cent. or 30 per cent. sucrose, almost all the grains germinate and the tubes begin to grow." This statement has since been found to be a bad mistake. For it is now clear that it was not true germination which was observed, but merely a protrusion of the contents of the grains in the form of very short irregular tubes, brought about by some degenerative change. True germination, to form tubes often over a millimetre long, has since been observed in cultures of pollen of stocks made in the traditional way on the surface of drops of nutritive agar: but the percentages of germination were very low.

The best germination was found on drops of 1 per cent. agar + 15 per cent. sucrose in conductivity water, with a little peptone. This medium was used in all the cultures of the following table except the first, which contained no peptone. The grains were placed in streaks on the surface of hanging drops of the medium by means of glass needles in sterile conditions. All the cultures were made strictly in pairs, one with pollen of a double-throwing ("d") cream race, and the other with pollen of a pure single ("no-d") cream. The two cultures of each pair were made at the same time, and with pollen from flowers of the same age. The pairs of cultures were examined after 2 days (except number (2), examined after 1 day): the temperatures varied between 60° and 70° F. Each culture was made with pollen from a different flower. The results are given in the following table.

The counts of the numbers of grains in the first five cultures are not very accurate: in the last five cultures, they are accurate to the nearest 5.

TABLE I.

Germinations on nutritive Agar.

Culture no.	Double-throwing cream ("d") Grains	Tubes	Percentage germination	Pure single cream ("no-d") Grains	Tubes	Percentage germination
1.	200	4	2	150	14	9
2.	700	25	4	350	22	6
3.	200	6	3	180	23	13
4.	350	14	4	420	32	6
5.	400	22	6	330	18	5
6.	315	36	11	257	39	15
7.	380	17	4	380	6	2
8.	350	26	7	323	14	4
9.	463	29	6	515	57	11
10.	150	12	8	149	19	13
Total	3508	191	Mean = 5·5 % $\sigma = 2{\cdot}54$	3054	244	Mean = 8·4 % $\sigma = 4{\cdot}20$

The mean percentages of germination are thus 5·5 per cent. for "d" pollen and 8·4 per cent. for "no-d" pollen. The standard error for the difference of the means is

$$e_{1-2} = \sqrt{\frac{\sigma_1^2}{n_1} + \frac{\sigma_2^2}{n_2}} = 1{\cdot}55.$$

The difference of the means, which is 2·9, is therefore 1·87 times its standard error. The chance that this difference might arise as an error of sampling is 1 in 16·2, so that it is only doubtfully significant.

The medium was found to have a pH of 7·4. In the last culture (No. 10) the pH was brought to about 6·6 with HCl, and a little agar was added. The result was that the tubes burrowed deep into the medium, instead of keeping close to the surface as in the other cultures.

In various other cultures, it was found that a piece of stigma placed in the medium did not noticeably increase germination. In two cultures of over 150 grains each, the cover slip was smeared with a crushed stigma, before the drop of agar was put on it: in these there was absolutely no germination.

It was thought that possibly the pollen tubes from "d" pollen might be found to fall into two visibly distinct classes. Accordingly an isolated culture of pollen of a "sulphur-white" race (a "d" race), that had given after 2 days the very good germination of 47 long tubes from 290 grains, was fixed and stained in Belling's aceto-carmine for 24 hours and then examined in strong chloral hydrate. (This combination was found to

give much better results than the traditional aceto-methyl-green). In 18 out of the 20 tubes examined, an elliptical nucleus could be seen near the end of the tube, made conspicuous by a pair of nucleoli. There was no indication of two visibly different classes.

The same nucleus, with its two nucleoli, can also be clearly recognised, with this staining combination, in the ungerminated pollen grain together with a second nucleus showing no nucleolus.

Now that meiosis in the stock has been shown by Allen (3) to be quite regular, a cytological study of the divisions in the pollen grain and tube seems desirable.

Since the percentages of germination on culture media were so low, a method was next devised for counting the germinations actually on the stigma. The stigmas of cut flowers standing in water were employed, for convenience and on account of the showery summer (1924). The papillae were carefully pollinated with pollen on glass needles, and the flowers were placed under a glass roof, exposed to a certain amount of sun. They were cut just before being used, when the stigmatic papillae were best developed—usually 3 to 4 days after the stamens had been removed.

The stigmas were examined after periods from 18 to 32 hours in the different tests. For staining, a solution of cotton blue in pure lactic acid was used, a stain recommended for pollen tubes by Guéguen (4). It was used in two strengths, 0·2 per cent. and 0·75 per cent. The stigma was first gently dipped into a drop of the weaker "lactic blue," so that many of the ungerminated grains were left in the drop. It was then cut with a clean razor into fairly thick transverse sections, which were transferred to the same drop of lactic blue. Counts were now made under the microscope of (1) the grains remaining on the razor, (2) those on the sections of stigma, (3) those free in the drop of stain. These together gave the total number of grains originally on the stigma (a). The sections were next stained on the slide in the stronger "lactic blue" for several hours or more, and then differentiated for a day or more in pure lactic acid, and finally examined in this medium. The total number of grains (b) now remaining on the papillae was first counted. The difference, $a - b$, represents ungerminated grains washed away with the staining fluids: for on germination the grains soon pierce the walls of the papillae with their tubes, and so are no longer washed away.

Next, with high-power objective, a count was made of the germinated and ungerminated grains on the papillae. Only those grains were considered as "germinated" whose tubes had begun to grow in length. The preparations showed up remarkably clearly, thanks to Guéguen's excellent

stain. The contents of the papillae were mostly not shrunk, and scarcely stained. The walls of the pollen tubes were perceptibly stained within the papillae. None the less, there were always some of the grains (usually a small minority) which, lying in unfavourable positions, could not be determined, whether germinated or not. The assumption was made that amongst these grains the proportion of germination was the same as amongst those that could be determined. If then the total number on the papillae were, say, 100, of which 70 could be determined and were found to be made up of 50 germinated and 20 ungerminated, the "estimated total germination" would be $50 \times \frac{100}{70}$. This explains the headings given in the table of results.

There remains one more class of grains to be considered, namely those attached to cut papillae, cut off by the razor and floating in the first drop of stain. In the last two tests, given below, these were counted and determined, and added to the others; but in the other five tests they were, by an unaccountable oversight, neglected. To judge from the last two tests, these grains would have raised the percentages in the earlier tests by from one-sixth to one-third of the values recorded. The omission certainly spoils the absolute values, but since the values for both kinds of pollen are affected by it, the comparison between them can still be made.

In each of the first two tests, two stigmas, closely similar in condition, were pollinated with pollen of "d cream" and "no-d cream" plants respectively. In the other six tests, for greater similarity of conditions, single stigmas were used, being pollinated with the one kind of pollen on the one side, and the other kind on the other. Afterwards they were cut in half longitudinally, and the various counting operations were made on the two halves separately. The stigmas belonged mostly to another, cross-bred, race.

The results are given in the following table:

TABLE II.

Germination on the Stigma.

	Pollen of double-throwing cream "d"				Pollen of pure single cream "no-d"			
Culture no.	Grains originally on stigma	Tubes counted	Estimated total germination	Percentage	Grains originally on stigma	Tubes counted	Estimated total germination	Percentage
1.	459	30	56	12	262	58	69	26
2.	265	59	70	26	712	95	461	65
3.	90	2	3	3	301	56	68	23
4.	83	8	9	11	92	9	10	11
5.	56	6	8	14	101	19	20	20
6.	230	61	67	29	250	85	98	39
7.	231	39	50	22	309	82	104	34
Totals	**1414**	205	263	Mean 16·7 % $\sigma=8{\cdot}58$	2027	404	830	**Mean 31·1 % $\sigma=16{\cdot}26$**

Comparison may again be made between the mean of the percentages of germination for "d" pollen, 16·7 per cent., and the mean for "no-d" pollen, 31·1 per cent. The standard error for the difference of the means is

$$\sqrt{\frac{\sigma_1^2}{n_1}+\frac{\sigma_2^2}{n_2}}=6\cdot 94.$$

The difference of the means, which is 14·4, is therefore 2·07 times its standard error, and the chance that such a difference might arise as an error of sampling is 1 in 26·25. But it may be noted that the percentages for the "no-d" pollen are also higher than those for "d" pollen in each of the tests considered separately, except in one where they are equal. The values for the two kinds of pollen are positively correlated, which indicates that part of the variability is due to varying conditions in the different tests—probably chiefly to differences in the stigmas. Thus the conditions for simple sampling are not fulfilled, and the results are really more fully significant than the above calculation would indicate.

These results, considered together with those of the cultures on agar, can scarcely leave any doubt that the germinating power of the pollen of the "no-d" cream race is higher than that of the "d" cream race. The two races seemed quite similar, but yet before the genetic significance of the result can be decided, comparisons of other pairs of "d" and "no-d" races seem needed. The need for caution is also indicated by the following isolated stigmatic test of pollen of the "d" race, not included in the table since not paired with any "no-d" test. The "estimated total germination" was 53 tubes from 157 grains, or 34 per cent. Since grains on free cut papillae were not included, the true percentage was probably a little higher, perhaps over 40 per cent. A single "d" test that gave well over 50 per cent. germination would of course disprove any theory that half of the grains fail to germinate, though it would still be possible that half might fail at some later stage between germination and fertilisation.

This opportunity may be taken to refer also to some further "counted-grain pollinations" made by the same method as those previously reported (2). It having been suggested to the writer that the most receptive part of the stigma was the summit, and not the lateral tufts of papillae, the grains were this time placed on the summit. Much larger numbers of grains were put on, usually over 100 to each flower. The proportion of seeds obtained was, however, even less than before, in spite of the very fine weather (July, 1923).

The summary of the results is as follows:

Race of pollen parent	Total number of grains	Number of flowers pollinated	Total number of seeds
"d" cream	902	7	15
"d" sulphur-white	909	8	6
"no-d" cream	988	10	12
"no-d" white	528	5	18

The proportion of seeds was thus so low that it seems that the most receptive part of the stigma is probably after all not the summit, but the sides, with their longer papillae, as was first supposed: indeed one of the flowers that set the greatest number of seeds (9) was one for which it was noted that the pollinating needle had accidentally slipped down on to one of the lateral tufts of papillae. It is these latter that were pollinated in all other experiments. The numbers of seeds were too low and "patchy" for any conclusion as to genetics.

The tests of germination on the stigma incidentally revealed one source of error in the method of "counted-grain pollination." For in one case the grains were counted on the pollinating needle, and the grains transferred from needle to stigma were found to be 263. But when the count of the total number of grains originally on the stigma was made, it was found to be only 157. Some therefore must have been simply knocked off by the papillae into the air.

In pollinations made out-of-doors, the number lost in this way would probably be greater, and this will go some little way to explain the low proportion of seeds obtained.

I wish to record my thanks to Mr H. Baker for kindly measuring for me the *p*H of culture media.

Summary.

1. Comparative tests have been made of the germination of pollen of stocks on nutritive agar. The mean percentage of germination was 5·5 per cent. for pollen of a double-throwing cream race, and 8·4 per cent. for that of a pure single cream race. The difference is statistically of only doubtful significance. The phenomenon previously considered as nearly 100 per cent. germination in sugar solution is not true germination.

2. Tests have also been made of germination on the stigma. The mean percentage was 16·7 per cent. for the double-throwing cream race and 31·1 per cent. for the pure single cream, the difference being significant. The possible interpretation of these results for the genetics of stocks is considered.

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GENETICS OF SEX IN *FUNARIA HYGROMETRICA*. A CORRECTION.

By E. J. COLLINS,

The John Innes Horticultural Institution.

In the *Journal of Genetics*, VIII. 1919, pp. 139–146, an account was given of some experiments on vegetative reproduction in the moss, *Funaria hygrometrica*. From these experiments I was led to conclude that cultures made from the male organs and the surrounding perigonial leaves of this monoicous form, produced pure male plants, and that a definite sex-segregation occurred in the haploid somatic tissue.

Independently, Correns, working with the same form, was led to a contrary conclusion, and my experiments have been repeated.

Spore cultures were established, and from the antheridia and surrounding leaves of the monoicous axes ultimately arising, vegetative cultures were again made. As a result, my previous conclusions cannot be maintained, and must be withdrawn.

In the first group of cultures I looked forward to the production of sporogonia as the indication of the presence of femaleness. None, however, appeared. I omitted to examine the axes minutely, and subsequent to the non-fertilization of the archegonia—which I must presume were present on small lateral shoots—a second crop of male flowering axes was developed. I therefore concluded, mistakenly no doubt, that the culture was wholly male.

In the repeated experiments cultures were maintained from which overhead watering was withheld, and a succession of leafy axes with terminal male "flowers" was obtained without the production of sporogonia. Such cultures had every appearance of being male. Close examination, however, always showed the small lateral branches bearing archegonia to be present. Similar plants, if watered overhead, developed not only the male "flowers" but sporogonia also, showing that they were in reality monoicous.

Thus it must be finally concluded that cultures derived from the haploid tissues associated with the male or female reproductive cells of the monoicous moss, *Funaria hygrometrica*, are alike in that the monoicous condition is again reproduced.

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THE ORIGIN OF CHROMOSOMAL MUTATIONS IN *UVULARIA*.

By JOHN BELLING,
Carnegie Institution of Washington, Cold Spring Harbor, N.Y.

(With Eleven Text-figures.)

CONTENTS.

INTRODUCTION.

AFTER some hundreds of chromosomal divisions have been observed in the pollen-mother-cells of a plant, certain so-called irregularities will doubtless have been met with, probably in proportions increasing with the extent of variation of temperature. These changes in the chromosome group may lead to the formation of exceptional plants of novel appearance, with different chromosome numbers, and different modes of inheritance from the parent stock (such as triploid or tetraploid heredity, instead of diploid). Abnormal forms of such origin have been and are being especially studied by various observers in the genera *Oenothera*, *Datura*, *Nicotiana* and *Hyacinthus*; while plants probably of similar origin have been investigated more or less in *Primula*, *Morus*, *Canna*, *Matthiola*, *Acer*, *Narcissus* and other groups. Among the commonest of these chromosomal changes are: (1) detachment, and subsequent elimination, of one chromosome or more at the first division of the pollen-mother-cell or the megasporocyte; (2) non-disjunction of one chromosome

pair, usually at the first maturation division; (3) non-conjunction, that is, two separate chromosomes instead of two combined ones, at the metaphase of the first maturation division; (4) non-reduction, or omission of the first division; (5) non-division, when the second maturation division would normally occur; and (6) fracture of a chromosome at the point of constriction, occurring occasionally at the first maturation division. Detachment, non-disjunction and non-division probably occur also in somatic cells. The study of these and other changes in the chromosome group may in time throw light on the causes of the differences in the chromosome groups of allied species; that is, on the evolution of the chromosome group, of which the evolution of the species itself may be sometimes in part a consequence. (Compare, for *Carex*, Heilborn, 1924.)

In the following pages an account will be given of chromosomal mutations which appeared in plants of *Uvularia* removed from a cold frame to a cool greenhouse in February. This greenhouse, which was devoted to Daturas, was more or less chilled at night, the fire being banked, and the night temperature consequently depending much on the external temperature and on the strength of the (mostly N.W.) winds, the glass panes as usual leaving chinks where they overlap. While the plants were growing, there was a cold spell for several nights (Feb. 23 to 25), preceded by a N.W. wind of over 40 miles an hour, and followed by a distinctly warmer period. Since the specimens of pollen showing non-division were prepared about a week after this cold spell, it is presumed that the cold may have caught the pollen-mother-cells of that bud in the maturation divisions. For there may well be an interval of over a week, judging from experiments with *Hyacinthus*, between the maturation divisions in the pollen-mother-cells and the first division in the pollen-grain, especially at cool temperatures. The specimen showing a large amount of detachment was prepared on March 13, and on March 11 and 12 there were N. and N.E. winds of over 40 miles an hour. The following table gives the minimum temperatures at the nearest U.S. weather sub-station, and the average wind velocities for the period in question.

Minimum temperatures at Roslyn, N.Y., and average wind velocities at New York City. (Extracted from the U.S. Dept. of Agr. Weather Bureau Reports.)

	February, 1924										March, 1924											
Date... ...	20	21	22	23	24	25	26	27	28	29	1	2	3	4	5	6	7	8	9	10	11	12
Minimum (degrees F.)	20	25	20	15	10	9	25	18	24	24	25	21	25	30	38	32	33	25	30	30	32	31
Wind (miles per hour) ...	27	35	27	24	13	7	7	18	25	19	14	12	13	16	6	15	13	39	23	17	34	38

CHROMOSOMES OF *UVULARIA*.

The chromosomes in the pollen-mother-cells and pollen-grains of *Uvularia* plants forced in the greenhouse have been observed by the writer for three years. The preparations of *Uvularia grandiflora* which are described in this paper, however, were obtained between March 1 and March 13, 1924. Young pollen-grains, at the metaphase of the division which separates the vegetative and generative nuclei, show the haploid group of 7 J-chromosomes remarkably clearly when treated with iron-acetocarmine (Fig. 1). These 7 chromosomes apparently all differ in size

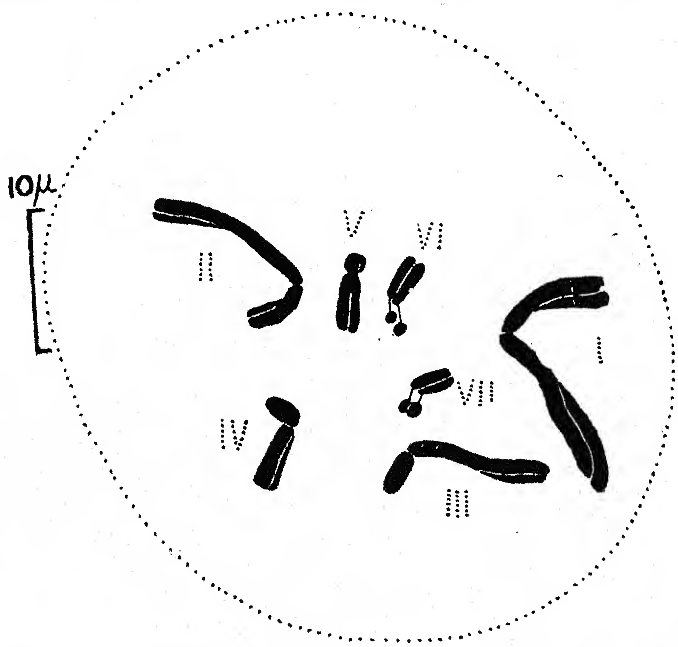

Fig. 1. Metaphase of the first nuclear division in the pollen-grain of *Uvularia grandiflora*, showing the seven chromosomes, each with the longitudinal split. (This pollen-grain was selected from a large number as showing the chromosomes especially clearly.) In each chromosome the spindle fibre was attached at the constriction, so that the constriction is usually turned towards the centre of the figure. The four larger chromosomes were outside the three smaller ones. The short segments of chromosomes VI and VII were obviously connected with the long segments by a fine thread.

This figure and the subsequent figures were drawn in outline with the Abbe camera, from preparations in iron-acetocarmine. The details were filled in from the microscope while the drawings were under a binocular magnification of 3·5. Zeiss' apochromatic water-immersion objective 70 was used, with the binocular attachment. A water-immersed Leitz' aplanatic achromatic condenser, corrected for water-immersion by a supplementary achromatic meniscus, was employed, with Wratten yellow-green light filter No. 56. The source of light was diaphragmed to fit the field of view. The attached scale of 10 microns was drawn from the projection of 0·01 mm. from an object micrometer on to the drawing surface. (Direct photographs of these chromosomes can readily be made, after squeezing the cytoplasm from the cell.)

or shape; II and III being probably different in length, while V and VI differ usually in the width of the gap between the segments. Each chromosome shows a clear constriction (compare especially Sakamura, 1920) from which as usual the spindle fibre proceeds; and this constriction in the two smallest chromosomes is sometimes longer than the chromosome, the two segments being connected by a single or double thread (as noted long ago in *Galtonia*, etc.). Below are found the relative lengths of the segments of each chromosome, measured in 3 haploid and 2 diploid pollen-grains; the numbers of each kind of chromosome varying from 6 to 8, according to how many were rejected because of foreshortening.

Chromosome	Long segment	Short segment	Total length
I	25	17	42
II	23	7	30
III	18	8	26
IV	10	4·5	14·5
V	7·5	2·5	10
VI	7	2	9
VII	4	2	6

(Camera drawings with an enlargement of 1870 were measured with dividers under a binocular magnification of 3·5, the unit being a millimetre. In these measurements the longer of II and III was in each case regarded as chromosome II.)

The positions of the constrictions in the constituent chromosomes of the bivalents in the pollen-mother-cells, show that, in all cases observed, homologous ends of the constituent chromosomes were apposed. At the late prophase and metaphase of the first division the same bivalents often assume different forms in different cells, as happens also in *Hyacinthus* (Belling, 1925), and doubtless in many other plants. Thus bivalent I may consist of two equal rings with two long free ends, in different planes (Fig. 2), resembling the double rings of the Orthoptera (Janssens, 1924); or it may form a large central ring with two smaller ones at the ends, somewhat as in Fig. 3; or one ring may be larger than the other. Bivalents II and III often consist of a small double projection at one side of the apposed constrictions of the constituent chromosomes, with a large ring in a plane at right angles, and two free ends again at right angles (Fig. 2). Sometimes the free ends are short or absent (bivalent II in Fig. 4), or the large ring may be absent altogether, as in bivalent IV of Fig. 2. The smaller bivalents may take the shape of truncated A's (Fig. 2). The separation of the chromosomes and chromatids of the bivalents will not be described here. The constrictions of the constituent chromosomes are always opposite, and the constituents are pulled apart

as usual by the spindle fibres attached at these constrictions. The constrictions are clearly seen in bivalents I and II of Fig. 3; in bivalent II the constituents on the side of the small segments have completely separated, but the other side of the metaphase ring is still fused, and the free ends show. Bivalent V, Fig. 3, is at the same stage. In Fig. 4, bivalent I has completely, and bivalent III nearly, separated into its constituents.

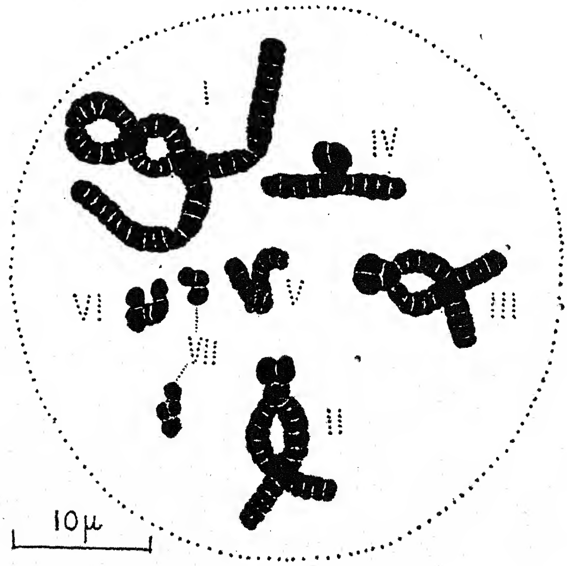

Fig. 2. A polar view of the late prophase to early metaphase in the pollen-mother-cell. Bivalent I is composed of two rings and of two long free ends, in different planes. Bivalents II and III also consist of three parts in different planes, while bivalent IV is formed of two such parts separated by the constrictions. The chromosomes of VII show non-conjunction. (Cells which depict this stage clearly are rare.)

Fig. 8 shows the anaphase, in which the longitudinal split has opened out in each constituent chromosome, producing double J's of different sizes, more or less corrugated like the metaphase bivalents from which they arose. There is an easy transition from this stage to that of four groups of 7 J-chromosomes each, passing into the four haploid pollen-grains (Fig. 1); or to two groups with 7 pairs of chromosomes each, passing into two diploid pollen-grains (Fig. 9).

DETACHMENT.

Detachment and subsequent elimination of one or more chromosomes, especially at the first maturation division, has long been known to occur

with more or less infrequency (*e.g.* in *Tradescantia,* Nawaschin, 1911). It may be seen abundantly in *Hemerocallis fulva* (Juel, 1897), and in other triploids, such as *Morus* (Osawa, 1920) and *Canna.* It has been especially investigated in *Datura.* In triploid *Datura stramonium,* detachment was found to vary, in the same plant, from 2·5 to 31 per cent., the increase being probably partly due to transient lowerings of temperature (Belling and Blakeslee, 1922). In diploid and in tetraploid *Datura* the amount of detachment was usually less than in triploids,

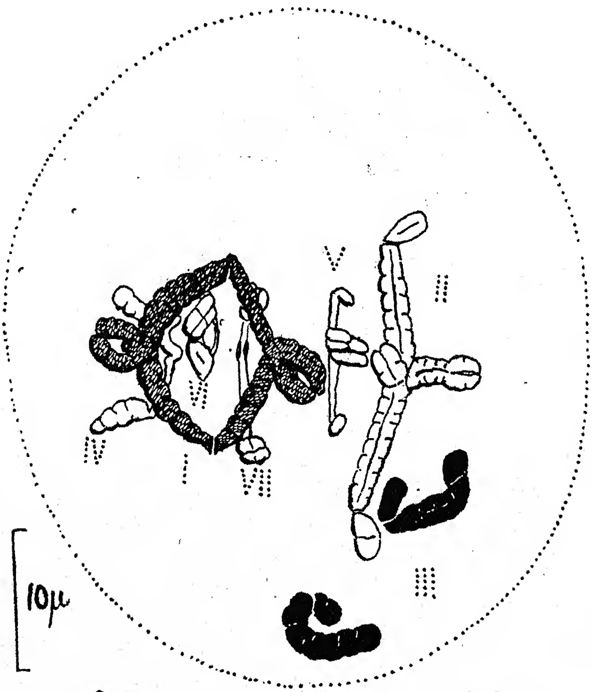

Fig. 3. Late metaphase to early anaphase. Bivalent I shows the constrictions at the fibre attachments in the large central loop. The two small lateral rings are apparently in the equatorial plane. Bivalent II shows the longitudinal splitting, and indicates that separate chromatids will disjoin from each of the two ends in the equatorial plane. Bivalents IV, V, VI and VII are advanced in their disjunction, that of VII being nearly complete. The chromosomes of III show non-conjunction, and both have gone towards the same pole.

ranging in tetraploids from 0 to about 6 per cent. in samples of over 400 pollen tetrads each (Belling and Blakeslee, 1924). Detachment in the microsporocytes or in the megasporocytes may be unimportant genetically, since the pollen-grains and embryo-sacs with $n-1$ chromosomes do not usually survive; as is shown, for instance, in the offspring

of the haploid *Datura*, or in the progeny of $2n-1$ branches. In *Cypripedium acaule*, pollen-grains with $n-1$ chromosomes were found to lag in their nuclear division, and perhaps did not proceed beyond the metaphase. Detached chromosomes, as is well known, either form miniature nuclei in miniature pollen-grains (microcytes), as in *Canna* and *Datura*; or they remain within the ordinary pollen-grains, as in *Uvularia* and *Hyacinthus*, in which case they are often visible in the resting stage as spherical micronuclei. The percentage of detachment can be reckoned from countings of the chromosomes at the second metaphase in the pollen-mother-cells, which gives the detachment at the first division; while by counting the pollen tetrads with microcytes or micronuclei we get the detachment at both divisions. A rough estimate of the total amount of detachment may be made by counting the microcytes or the micronuclei in a sample of pollen.

Buds of *Uvularia grandiflora* from plants forced in the late winter showed varying amounts of detachment, usually small. But in one case 70 pollen-mother-cells out of 100 examined showed one or more detached chromosomes, or segments of chromosomes, after the first or second maturation division. In this bud, 31 pollen-mother-cells showed one detached chromosome or segment, 32 showed two chromosomes or segments of chromosomes lying loose in the cytoplasm, 3 cells showed three, and 4 cells showed four detached chromosomes or segments; while only 30 cells out of the hundred were free from detachment. In the diploid pollen-grains also detachment sometimes occurred (Fig. 10).

NON-DISJUNCTION.

The delayed separation of a pair of chromosomes at the first maturation division, so that they both pass to one pole, produces in the pollen-mother-cells two groups of anaphase or second-metaphase chromosomes, $n-1$ and $n+1$ in number. A case of true non-disjunction can usually be identified as such at the early anaphase of the first maturation division, while at the later stages it cannot be distinguished from non-conjunction. Non-disjunction was long ago observed in the diploid *Oenothera* (Gates, 1908), and also in *Crepis* (Rosenberg, 1918); while its effects have been fully studied in *Drosophila* (Bridges, 1916, 1921). A special counting of over 500 pollen-mother-cells (by Miss A. D. Bergner), in the diploid *Datura*, showed only three cases of apparent non-disjunction. Three contiguous cells had each $11+13$ chromosomes, in the second metaphase. This was evidently induced by some common cause (Belling and Blakeslee, 1923). In 1137 pollen-mother-cells of diploid Daturas

there were found only 8 cases of non-disjunction after the first division, which is about 7 cases in 1000. This non-disjunction (primary non-disjunction of Bridges) whether at the first division or at the second division of the pollen-mother-cells, in the embryo-sac mother-cells, in the young pollen-grains, or in the somatic tissues of the plant, is doubtless a cause of the appearance of $2n + 1$ plants in *Oenothera, Datura, Nico-*

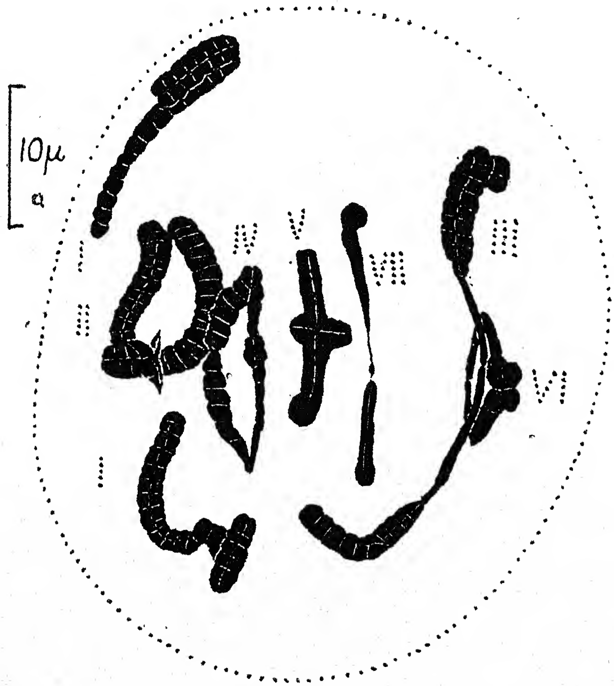

Fig. 4. First metaphase to early anaphase in the pollen-mother-cell, showing the lagging of bivalent II, when bivalents I, III and VII have already disjoined, or nearly disjoined, and IV, VI, and even V, are well on their way to disjunction. The ring formed by bivalent II is nearly in the equatorial plane, so that if disjunction took place, most of one chromatid from each constituent chromosome would probably go towards each pole. A small loop may be observed beginning to form at the points of constriction of bivalent II. (Many clear figures showing stages similar to Figs. 3 and 4 were obtained from one bud.)

tiana, etc. However, as already mentioned, the total of cases usually classified as non-disjunction is composed of the cases due to non-disjunction in the strict sense, plus those due to non-conjunction.

In *Uvularia grandiflora*, at the first maturation division, the constituent chromosomes of the bivalents are pulled polewards into loops, starting from the points of constriction (Figs. 3 and 4). Normally the

separation of the chromosomes seems to begin nearly simultaneously in the 7 bivalents; but, under an abnormal environment, such as a lowered temperature, one (or more) of them may be retarded from the start (Fig. 4). The smaller bivalents usually complete their separation before the larger ones; which seems natural, since there is a shorter length to be separated.

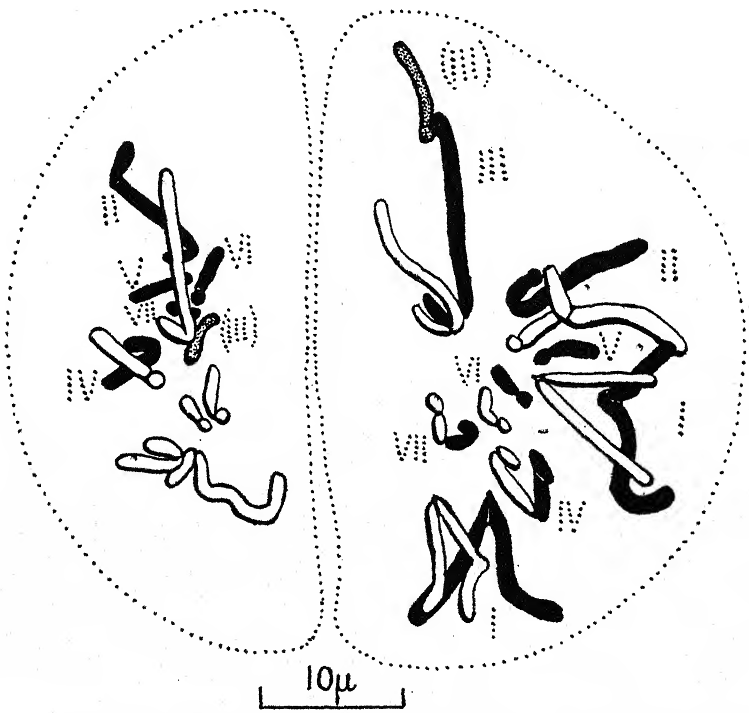

Fig. 5. Early anaphase of the second division in a pollen-mother-cell. Non-disjunction had taken place at the first division, so that both split chromosomes I went to the right-hand side. On the left hand the larger segment of one chromatid of bivalent III was broken at the constriction during the first division, and remained attached to the corresponding chromatid. It was thus carried to the right-hand side. (The two portions of this chromosome are stippled in the figure. The upper group of chromosomes on each side is shown in outline only.)

On the whole, non-disjunction (in the wide sense noted above) of chromosome I has been seen 5 times; of chromosome II, once; and of chromosomes V or VI, 4 times. Three of these 10 cases of non-disjunction were observed in the pollen-mother-cells, and the remaining 7 in the pollen-grains. In Fig. 4 bivalent I has separated into two chromosomes, and bivalents III, IV, V, VI and VII are well advanced in separation.

But bivalent II shows only a minute loop starting at the points of constriction. This chromosome pair will probably be so late in separating that it will not disjoin before all the others have gone to the poles, and the two halves may hence be left on the same side. In another early anaphase from the same bud, bivalent I was in the same state as bivalent II in Fig. 4; while the other bivalents in the same cell were well advanced

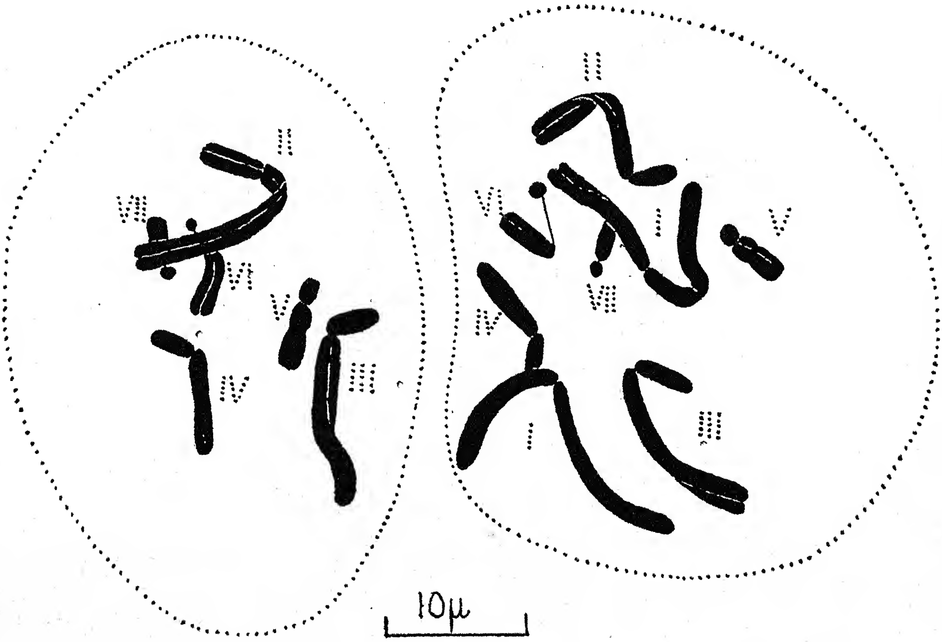

Fig. 6. Two pollen-grains of a tetrad, that were found still connected by their outer coats (which are not drawn). The dotted line marks the boundary of the cytoplasm. The chromosomes overlap somewhat, but their numbers and classes are perfectly recognizable. The right-hand cell contains two individuals of chromosome I, which chromosome is absent from the left-hand cell. The cells depicted in Fig. 5, if they had been allowed to proceed in their development, would doubtless (apart from the presence of a fracture) have given rise to two pollen-grains with eight chromosomes and two pollen-grains with six chromosomes, chromosome I being the supernumerary (or the deficient) chromosome. On the right-hand side, the small segment of chromosome VI is at nearly the observed maximum of distance from the larger segment of the same chromosome. The difference in this respect between V and VI is well seen in this figure.

towards a complete separation of their constituents. In several other early anaphases, in which all the bivalents were carefully examined, the chromosome pairs disjoined more or less uniformly. Non-disjunction is of course readily discernible at or after the second division in the pollen-mother-cell, though not distinguishable from non-conjunction. An

examination of a small number of metaphases and early anaphases of the second maturation division yielded one case of non-disjunction, shown in Fig. 5. Here the halves of the split chromosomes (chromatids) of the second metaphase have just separated. On the right-hand side there are 8 chromosomes in each group, including two of number I. On the left-hand side there are, in correspondence, only 6 chromosomes in each group, chromosome I being absent. (There is also a fracture of chromosome III visible in the cell, which will be described later.) These three cases of non-disjunction obviously occurred at the first division.

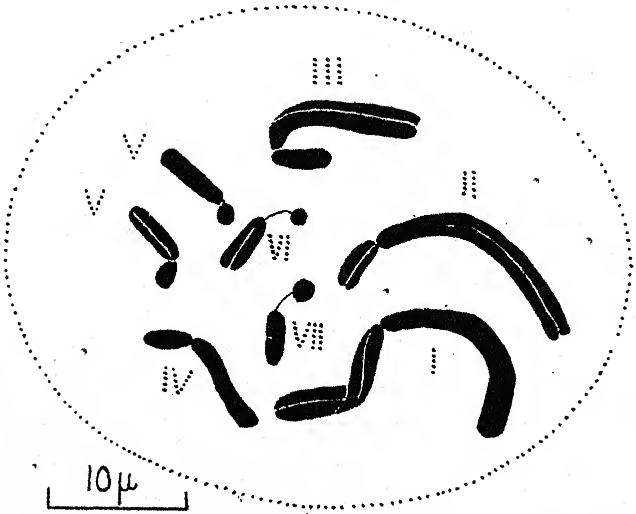

Fig. 7. A single pollen-grain showing an extra chromosome V. One of the chromosomes V shows the longitudinal split for the next division. The other (like IV and VII) is not rightly placed for the split to be visible. The chromosomes are well separated in this cell, and it may be noticed that, as usual, the two smallest are near the middle of the group.

In 104 young pollen-grains from one bud, at the metaphase or early anaphase of the division which separates the vegetative and generative nuclei, all the chromosomes were clearly distinguishable, and could be counted and classified with certainty. Seven of these pollen-grains showed an extra chromosome, resulting from non-disjunction, probably at the first division in the pollen-mother-cell (or arising perhaps from non-conjunction). Assuming that the non-disjunction whose results are seen in these pollen-grains happened at the first division; then, as Fig. 5 shows, one pollen-mother-cell showing non-disjunction should produce two pollen-grains with $n + 1$ chromosomes, and two pollen-grains with $n - 1$ chromosomes. The pollen-grains with $n - 1$ chromosomes may, as

already mentioned, be later in dividing than the normal ones. Hence fewer could be counted in this preparation, which showed a majority of n-chromosome grains that had not begun nuclear division. In fact, only one pollen-grain with 6 chromosomes was found among the 104 countable grains. This is shown on the left hand of Fig. 6. Hence the 6 cases of $n + 1$ pollen should correspond on the average to 3 pollen-mother-cells, and the one pollen-grain with $2n + 2$ chromosomes (Fig. 11) to 1 pollen-mother-cell; while the 85 pollen-grains with n chromosomes should correspond to 21·25 pollen-mother-cells, and the 11 pollen-grains with $2n$ chromosomes (Fig. 9) to probably 5·5 pollen-mother-cells. Here we have 4 pollen-mother-cells showing non-disjunction out of a total of 30·75, which is 13 per cent.; a remarkably large amount as compared with the ordinary 0·7 per cent. in diploid *Datura stramonium*. Examination of pollen and pollen-mother-cells of *Uvularia* in the first months of 1923, when the plants were forced in the same way as in 1924, disclosed no such abundance of non-disjunction. In fact the high percentage of non-disjunction in 1924 followed a marked fall and subsequent rise of temperature.

Non-conjunction.

This term is used instead of non-conjugation, because in most cases it cannot be told whether conjugation, that is, parasynapsis, has taken place or not, with regard to the chromosome pair in question. As already stated, non-conjunction cannot be distinguished from true non-disjunction, in the later stages. If the two homologous chromosomes which form a bivalent remain separate, they may presumably go to opposite poles in half the cases, and in half the cases to the same pole (Fig. 3). Non-conjunction of course differs from non-disjunction in not occurring at the second division, or at divisions in the pollen-grain, or in somatic tissue. It is possible and indeed probable that much of the non-disjunction calculated to occur in tetraploids at the first division (Belling and Blakeslee, 1924) is due to the non-conjunction of one or more of the four chromosomes of any quadrivalent. A certain amount of this kind of non-conjunction has also been observed to occur in triploids, and in the 3-chromosome set of $2n + 1$ plants. Non-conjunction is abundant, as is well known, in the early generations of some species hybrids or presumable species hybrids, such as the *Cannas* "Austria" and "Italia," where only a few bivalents usually appear at the first metaphase, the rest of the 18 single chromosomes showing non-conjunction, which in this case is probably also non-conjugation. Other probable species hybrids among

Cannas, with approximately the triploid number of chromosomes, such as "Pennsylvania," "Indiana," and "Louisiana," also show much non-conjunction.

Among the *Uvularia* material, two cases of undoubted non-conjunction were met with. Fig. 2 shows a case of non-conjunction in the late prophase or early metaphase. The constituents of six of the bivalents are apposed, but bivalent VII consists of two separate chromosomes. It cannot of course be told whether these two would have moved to the same or different poles, or whether one or both would have been detached from the chromosome groups. Fig. 3 shows also six bivalents, but the chromosomes which should form bivalent III are separate, and by the position of the constrictions it seems evident would have both gone to the same pole, which one has already attained. Few cases of non-conjunction have been observed in diploid daturas, cannas or hyacinths. There is no indication that the univalents divide at the first maturation division, as happens in hybrid wheats, for instance; and in Fig. 3 they apparently do not.

NON-REDUCTION.

Non-reduction may occur at the metaphase of the first division of the pollen-mother-cell or megaspore-mother-cell. It amounts to the omission of the division of the chromosome group, but not of the individual bivalents. The bivalents separate into two chromosomes each at the equator, and then a chromosomal and nuclear division takes place with the $2n$ chromosome number, each chromosome splitting lengthways, and the $2n$ separate chromosomes passing to each pole. Thus two pollen-grains, instead of four, are formed from each pollen-mother-cell; each grain containing $2n$ chromosomes, and having twice the normal amount of cytoplasm. These chromosomes, from the method of their formation, are not necessarily in connected pairs. As measured under the microscope when they are young and full of cytoplasm, the diameters of such giant pollen-grains are about one-and-a-quarter of those of the corresponding normal grains which have each only a quarter of the cytoplasm of the pollen-mother-cell and n instead of $2n$ chromosomes. The process of non-reduction has been observed in *Morus* (Osawa, 1920), in *Canna*, and in *Datura*, being especially clear in triploids. (In *Papaver*, Yasui (1921) thought that the double number was produced by the two nuclei fusing again after the first maturation division.) The presence of giant pollen-grains, which is not uncommon in samples of pollen, points either to the occurrence of non-reduction, or to the

omission of the second maturation division. In the anthers of plants which have been exposed to temporary chill in the spring or autumn, double-sized pollen-grains may often be found on search. Out of about 3500 pollen tetrads examined from triploid daturas, nearly 1 per cent. had two giant grains; while among about 6500 pollen tetrads of tetraploid

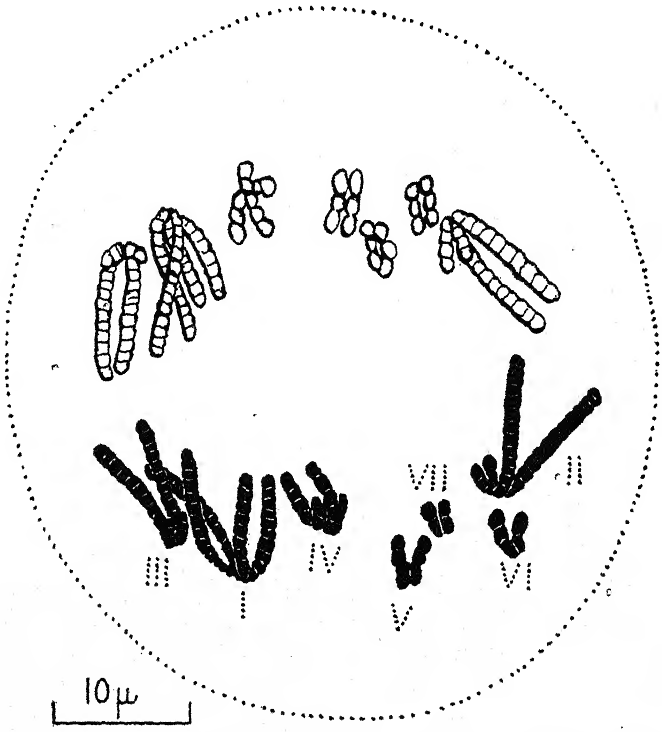

Fig. 8. Anaphase of the first division in the pollen-mother-cell. This figure is inserted for comparison with Fig. 9 especially. The chromosomes proceed to the poles as double J's with the split halves firmly attached at the points of constriction. It is obvious that if this cell divided only once, and the two J's in each case became slightly loosed from their mutual adhesion, there would be two double pollen-grains formed, such as the one depicted in Fig. 9. The corrugation of the chromosomes in perfectly-fixed preparations is as well marked in this stage as in the metaphase.

Daturas, 0·2 per cent. had two giant grains instead of four of normal size (Belling and Blakeslee, 1922, 1924). In normal diploid Daturas, non-reduction is usually rare. Non-reduction in diploids can be distinguished from non-division (omission of second nuclear division) by the presence in the pollen-mother-cell of only one metaphase plate which contains $2n$ chromosomes splitting lengthways, or by the presence of

two anaphase groups of $2n$ single chromosomes each. *Uvularia grandiflora* afforded an example of the formation of many double-sized pollen-grains, doubtless as a result of temperature changes, but in only one such cell were the chromosomes so loosely paired that the doubling was possibly, but not probably, due to non-reduction. De Mol observed

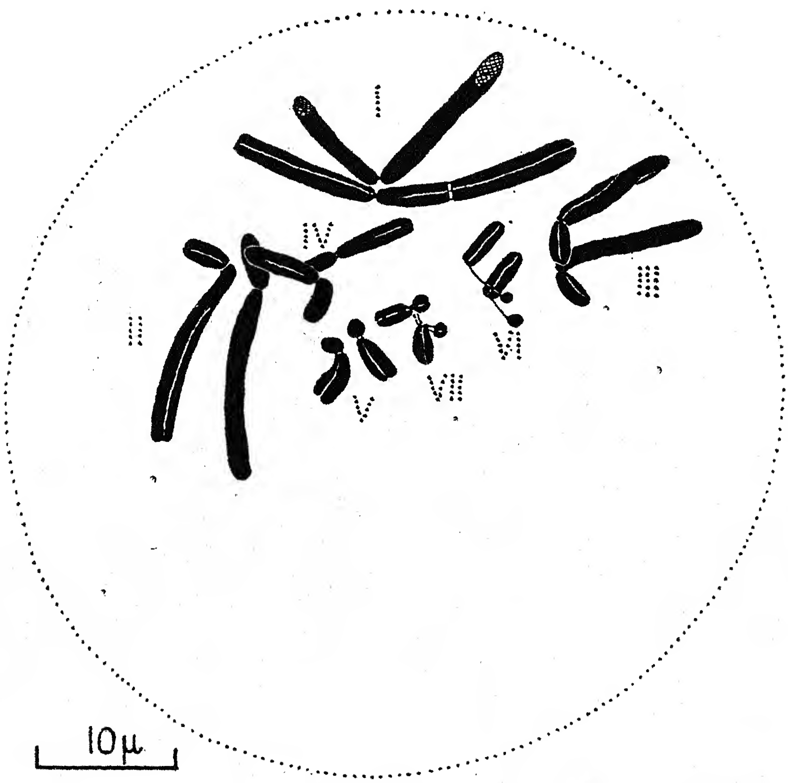

Fig. 9. One of the giant pollen-grains showing the 14 chromosomes, all split longitudinally for the first division in the pollen-grain. In the double pollen-grains which were observed, with one exception, the members of each of the pairs of chromosomes were in close proximity, showing that they had but lately been in the state portrayed in Fig. 8. It is noticeable that the members of the pairs do not adhere, with the exception of VII which shows a connecting thread. Measurements of several of these double pollen-grains at this stage showed that they had about one-and-a-quarter the diameter of the haploid grains.

giant pollen-grains in diploid hyacinths raised in a greenhouse (1923). About ten years ago, the writer was daily examining the pollen of crosses of *Stizolobium* (*Mucuna*), from an acre of F_2 plants and an acre of F_3 sibships. A cold wind in the autumn sent down the temperature for a

short time. A few days after the return of warm weather, a number of plants examined showed many double-sized grains mingled with the normal pollen, and occasionally a quadruple-sized grain. The grains clung slightly together, the normals in fours, and the double-sized in pairs, while the quadruple grains were single (Compare Borgenstam, 1922, on doubling of chromosomes by cold in *Syringa*; and also Bowen, 1922, on abnormal mitoses in insects.)

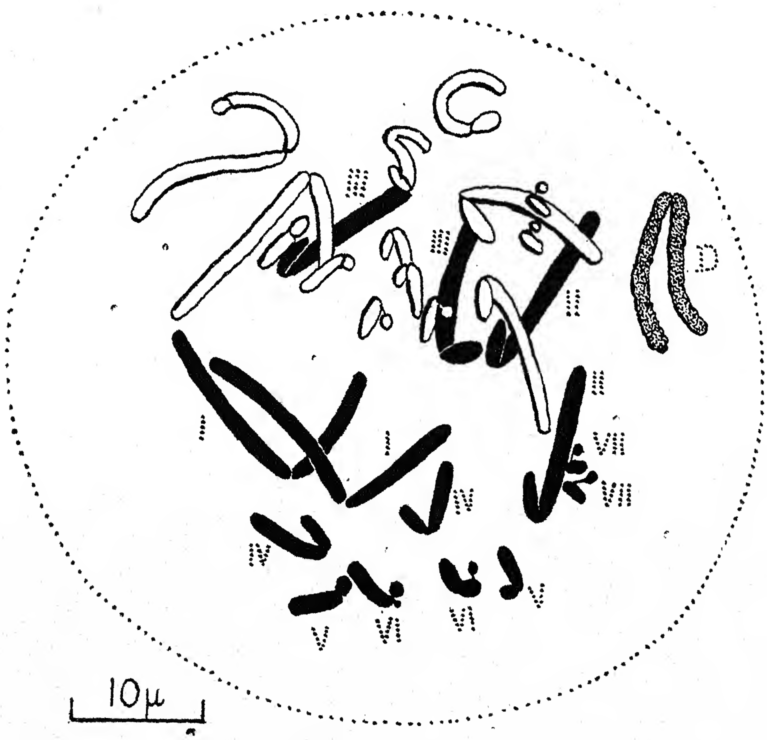

Fig. 10. Diploid pollen-grain at the anaphase of the first division. The nearer chromosome group is given in outline only. The degenerating detached chromosome to one side is probably an unsplit chromosome I, rather than a split II or III. It is in a different plane to either of the two groups, and outside the spindle. It was evidently detached at the first and only division in the pollen-mother-cell.

Non-division.

It has not been directly demonstrated that this occurs in the pollen-mother-cells of *Datura*. However, in *Uvularia*, conditions are more favourable for its detection, there being certain criteria by which non-reduction, or omission of the first division, can with sufficient probability

be distinguished from non-division, or omission of the second division. In fact, in *Uvularia*, omission of the second cytoplasmic and nuclear division in the pollen-mother-cells is apparently a usual method of doubling the chromosome number, and is probably occasioned by a temporary chill. As already stated, in *Uvularia*, no case of doubling of

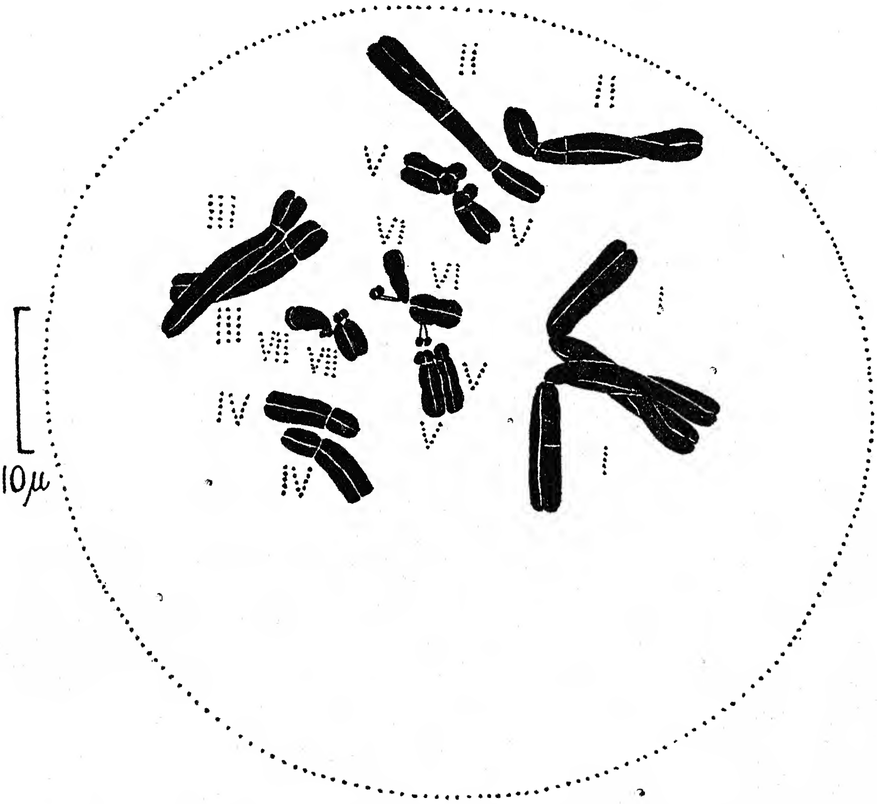

Fig. 11. This pollen-grain had been subjected to pressure, and the apparent breadth of the chromosomes was in consequence increased. Because of the flattening-out, it could be established that the members of the two pairs of chromosome V showed a longitudinal split, which indicated that there were two pairs of dividing chromosomes, not two divided chromosomes. This grain thus exhibits the combined effects of non-disjunction (or possibly, non-conjunction) and of non-division.

the chromosomes by non-reduction was certainly observed. Among the 104 pollen-grains whose chromosomes were counted, there were, as has been already indicated, 92 grains with n (or $n+1$, or $n-1$) chromosomes. There were also 12 double-sized grains with $2n$ (or in one case, $2n+2$) chromosomes. The 92 pollen-grains correspond to 24·25 pollen-mother-

cells, and the 12 giant grains to probably 6·5 pollen-mother-cells, allowing as before for the absence of $n - 1$ and $2n - 2$ grains. Thus the proportion of pollen-mother-cells with non-division would be here 21 per cent. The many double-sized pollen-grains which were not at the metaphase stage had mostly two nuclei, while the bulk of the normal grains showed only one nucleus. This indicated that the diploid grains were ahead of the haploid grains in completing their nuclear divisions.

Fig. 8, the anaphase of the first division, may be compared with Fig. 9, the diploid pollen-grain, and also with Fig. 5, the early anaphase of the second division. It will be seen that by the omission of the second division the chromosomes would be left in pairs, as shown in Figs. 9 and 11. In non-reduction the chromosomes in the diploid pollen-grains are not in definite pairs. If non-disjunction happened at the first division, then the extra chromosome would split as usual in the anaphase, and all the chromosomes be in pairs in the diploid pollen-grain resulting from non-division, resembling the second anaphase shown in the right-hand cell of Fig. 5. This corresponds with Fig. 11, which shows both non-disjunction and non-division. In two of the 12 diploid pollen-grains there was a detached chromosome at one side of the cell. One of these cells is depicted in Fig. 10. Here the chromosomes are separating into two groups of 14 each at the anaphase, and the detached chromosome at one side of the cell is degenerating. Hence there are three reasons for considering these diploid pollen-grains the result of non-division, rather than of non-reduction.

Fracture.

Fracture of a chromosome usually occurs, in the plants studied, at the constriction. Especially in those chromosomes of *Uvularia* where the constriction may be extended into a thin thread (compare the chromosomes of *Galtonia*, as described by several observers, and lately by Newton, 1924), cases of fracture have been seen, where the two segments have passed into different cells. The loss of such a segment of a chromosome might lead to a case of genetic "deficiency" (Bridges, 1917), if the gametes with the segment missing were viable, and if the spindle-fibre attachment of the shortened chromosome was normal. The writer can confirm the common occurrence of a phenomenon of the nature of fracture in *Secale*, described fully by Gotoh (1924). In *Uvularia*, fracture of chromosomes at the constriction was observed in one pollen-mother-cell, in three pollen-grains, and in several cells showing detachment (omitting some doubtful cases). In Fig. 5 one of the two split

halves (chromatids) of chromosome III at the first maturation division broke at the constriction, the long segment going to the wrong pole, attached in a reverse direction to the apposed chromatid of the other constituent chromosome of bivalent III. The short segment of this fractured chromatid alone accompanied its fellow chromatid to the other pole. (Obviously the chromosomes were already split when the first maturation division took place.) If the attached segment remained attached, and split lengthways with the chromosome to which it was fused, it would probably parallel the genetic results obtained by duplication of a portion of a chromosome (Bridges and Morgan, 1923). In one pollen-grain the small segment of chromosome V (or VI) was missing. In two pollen-grains an extra loose-lying small segment of a chromosome was visible, belonging to one of the chromosomes V, VI or VII. In these three cases fracture of a chromosome at the constriction had doubtless occurred in the pollen-mother-cell, the two segments having gone into different microspores. In the bud which showed 70 per cent. of cases of detachment in the pollen-mother-cells, several of the detached chromosomes, either in the vacuolated or in the spherical form, were too small to be single chromosomes, and were probably detached small segments of chromosomes V, VI or VII.

DISCUSSION.

The bearings of chromosomal mutations on the science of genetics may be threefold. The study of the genes in their relation to each particular chromosome, or segment of a chromosome, when deficient or in excess, adds to the proofs of the chromosome theory of inheritance. Some of these chromosomal mutations, especially tetraploidy and hexaploidy, may play a part in the striking changes of the chromosome group from species to species, shown for instance in the genus *Chrysanthemum* (Tahara, 1921). The formation of triploids and tetraploids may also be of practical value in other cases besides the large-flowered and nearly seedless triploid Canna and hyacinth clones among ornamental flowering plants, and the more or less parthenocarpic triploid mulberries among fruit trees.

The hypothesis that non-disjunction leads to the permanent formation of $2n + 2$ strains, encounters the manifest inconstancy of the $2n + 2$ *Datura* and *Nicotiana* (Clausen and Goodspeed, 1924). It has been assumed (Heilborn, 1924) that the univalent chromosomes of the genus *Carex* in cases of non-conjunction would divide at the first division, but the fact has yet to be ascertained. Non-reduction, non-division in the

germ-cells, and somatic non-division, are doubtless causes for the formation of tetraploids and triploids, and for the doubling of the chromosome number occasionally in F_1 hybrids with non-conjugating chromosomes (Blackburn and Harrison, 1924). Tetraploids of flowering plants seem, however, inconstant. The progeny of a true tetraploid *Datura* included 11 per cent. of forms with aberrant chromosome groups (Belling and Blakeslee, 1924 *a*). Observations on triploids and tetraploids will add to our knowledge of the mutual relations of chromosomes in the formation of trivalents and quadrivalents. Triploids provide a copious source for $2n + 1$ plants of all kinds. In one species of plant at least fracture seems to be the demonstrated cause of an increase in the number of chromosomes. Cases of fracture of a chromosome at the constriction and attachment of a segment to another chromosome are worthy of investigation to see if they afford a means of permanent increase in chromosome length. In this connection the secondaries of $2n + 1$ Daturas are of interest (Belling and Blakeslee, 1924 *b*).

SUMMARY.

(1) *Uvularia grandiflora* and *U. perfoliata* were forced in a greenhouse which was cooler at night. During the early months of two successive years no extensive aberrations were noticed. In the third year, apparently on account of excessive changes of temperature, abnormalities of chromosome distribution were marked.

(2) In one bud 70 per cent. of the pollen-mother-cells showed one or two (and sometimes more) detached chromosomes, or segments of chromosomes. The other buds examined had only a small percentage of such cases.

(3) In three other buds, ten cases of non-disjunction were observed. This non-disjunction was shown, in three cases, to occur at the first division in the pollen-mother-cell. It affected chromosome I, the largest chromosome, in half the cases. In one bud, non-disjunction was calculated to have occurred in 13 per cent. of the pollen-mother-cells from which those pollen-grains whose chromosomes were counted had arisen.

(4) Two undoubted cases of non-conjunction were seen. It is possible that some of the cases later than the first division, reckoned as non-disjunction, were due to non-conjunction.

(5) In one bud an extensive doubling of the chromosome number was observed. Of those pollen-grains whose chromosomes were counted the giant pollen-grains formed nearly 12 per cent. This doubling is

considered to have taken place by the omission of the second nuclear and cytoplasmic division.

(6) There were observed four cases of fracture of a chromosome at the constriction, in which the two segments had passed into different cells. In one such case the detached segment was attached to the end of the corresponding chromatid, homologous ends being apparently apposed.

(7) The phenomena of aberrant chromosome distribution observed in these *Uvularia* plants were of a nature to lead to the possible production of plants with chromosome groups of $2n + 1$, $2n + 2$, $3n$, $3n + 1$, $3n - 1$, $4n$, $4n + 1$, $4n - 1$, $4n + 2$, $4n - 2$, etc.; besides plants showing duplication of a segment of a chromosome.

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GENETIC STUDIES IN POTATOES: McKELVIE'S ARRAN VICTORY MUTATIONS.

By R. N. SALAMAN, M.A., M.D.

(With Six Text-figures and Two Coloured Plates.)

At the International Potato Conference in November 1921 Mr McKelvie of Arran read a paper (3) on and showed specimens of a series of mutations or tuber sports that he had discovered in a crop of the self-coloured purple-skinned variety, Arran Victory (Fig. 1, Pl. VI). The mutated tubers formed a series beginning with a more or less uniform dilution of the deep purple pigment to a pinkish purple over the surface of the tuber (Fig. 2, Pl. VI) followed by a mottled coloration where, between the patches of more or less full purple, a pinkish purple colour was developed in the skin (Fig. 3, Pl. VI). From this stage the next was developed by the omission of the intervening pinkish purple (Fig. 4, Pl. I); and this was succeeded by the suppression of the definite purple patches resulting in a mutation with white tubers and an occasional small patch of colour, followed finally by the stage in which all the tubers were of a pure white skin.

Loss of colour, complete or partial, has been recorded often before, and Mr McKelvie's series of tubers would have differed from their predecessors only in the more complete records of observations he was able to give, had he not made a further observation of outstanding importance.

The green tops of the mutant forms were, according to Mr McKelvie, indistinguishable from that of Arran Victory, except in the case of the white tubered plants, which he first raised in 1921 (see Text-fig. 3). These plants in 1921 and in subsequent years have displayed several character-differences of importance. Not only was there much less pigment in the stem and the plant generally, but their growth was shorter and less vigorous than those of Arran Victory. More striking, however, was the definite alteration in the shape of the leaflets described by Mr McKelvie. It was clear that the sport was not confined to a mere variation in the development of colour in the tuber, or of that in the plant generally, but according to Mr McKelvie, these changes, in conjunction with that

of the leaves "constitute a new and distinct variety if they prove to be permanent."

The views put forward gave rise to lively discussion both at the time and afterwards. The older view enunciated by Sutton (8) and expressed so unequivocally as follows: "I would only say in closing that the more deeply the subject is investigated, the more convinced one becomes that there is no ground for believing nature ever has given rise to any New and Distinct variety of potato by Bud-Variation" has been endorsed by East (2) who, however, expresses himself rather more guardedly and points out that such authentic tuber mutations of which there are records are examples of the "losses of a dominant or epistatic character allowing the appearance of a recessive or hypostatic character."

These views have held the field up till now in the world of Potatoes.

Some have not hesitated to ascribe the occurrence of McKelvie's white-tubered variant to the presence of a rogue or of a tuber left in the ground from a previous crop introduced in error. To me the facts adduced seemed too weighty and the reputation of the observer too well established to allow of any such hasty view. I accordingly asked Mr McKelvie whether he would allow me to grow on some of his material and make my own observations. This he most kindly agreed to do, and it gives me very great pleasure to express my sincere thanks to him for this act of courtesy, as well as for the assistance he has accorded me in my efforts to get a clear account of the whole story. That the results of my experiments convince me of the absolute correctness of Mr McKelvie's view is an additional satisfaction.

The problem raised by McKelvie's sports is of fundamental importance, and one may perhaps be excused if one treats it in some detail.

It may be objected that to call the variations involved "Mutations" is a begging of the question, but it would seem to be even more open to objection to call them "colour variations." The issue raised by Mr McKelvie is, whether a new variety can be brought about as a result of bud variation. This leads one to the further question as to what constitutes a new and distinct variety. Strictly speaking, a permanent and recognisable change of character, whether it be one affecting the tubers below ground or the stem and leaves above, is difference enough. There would seem to be no *a priori* grounds to relegate a change of colour distribution in the tuber to the category of a mere variation, whilst a change of foliage character is to be held sufficient to constitute a varietal difference. The question of permanence is, of course, of

paramount importance in the consideration of such a question, nor can that of the extent of the change be left out of the question. The distinction between one variety and another must be real and measurable, nor must one forget to be practical in respect to so mundane a subject as the potato. The Synonym Committee of the National Institute of Agricultural Botany have accorded Field Marshal and Sefton Wonder varietal rank, though the one differs from Up-to-date, and the other from Great Scot, merely in the possession of a thickened, corky periderm to the tuber, giving the latter a heavily russeted appearance. Similarly, the change of flower colour from heliotrope to white alone differentiates the two varieties President Kruger and General. In both cases the differences are readily observed and permanent.

Mr McKelvie claims varietal rank only for his No. 3 Mutation, but logically he might claim it for his No. 1, and very possibly for his No. 2. In short, the decision as to whether one permanent difference or several differences shall justify varietal rank or not, must rest with the commonsense of the observer; it does not raise a scientific issue.

Many important problems are raised by Mr McKelvie's series in regard to the nature of the colour changes which have taken place. Are the alterations observed in the foliage and elsewhere consequent on the loss of colour factors, or is it due to some further genetic disturbance, chromosomal or cytoplasmic? Are the disturbances localised in the embryonic tissue of the tuber buds, or are they equally present in the germ cells of the ovary and anther? Is the loss of factors, if such there be, common to the whole plant, or is the variant plant a mosaic?—a suggestion which was made by Mr J. W. Lesley in the discussion which took place at the Conference when Mr McKelvie first showed his specimens. It was with the hope of throwing some light on these issues that I asked Mr McKelvie to furnish me with the material which I have studied during the last three years.

Mr McKelvie described three mutations in detail and he gave me tubers of all, as well as certain additional material.

DESCRIPTION OF THE MUTATIONS.

Mutation 1 (A.V.V. 12). In the 1919 crop of Arran Victory was found a tuber of normal shape issuing from a typical Arran Victory plant, whose pigmentation was peculiar. The tuber was coloured the usual purple over one-half of its surface, whilst the remainder was white, the division between the two halves being more or less longitudinal. This abnormal tuber is in error represented in Fig. 2, p. 35, of the Report of

ARRAN VICTORY. MUTATION No. 12.

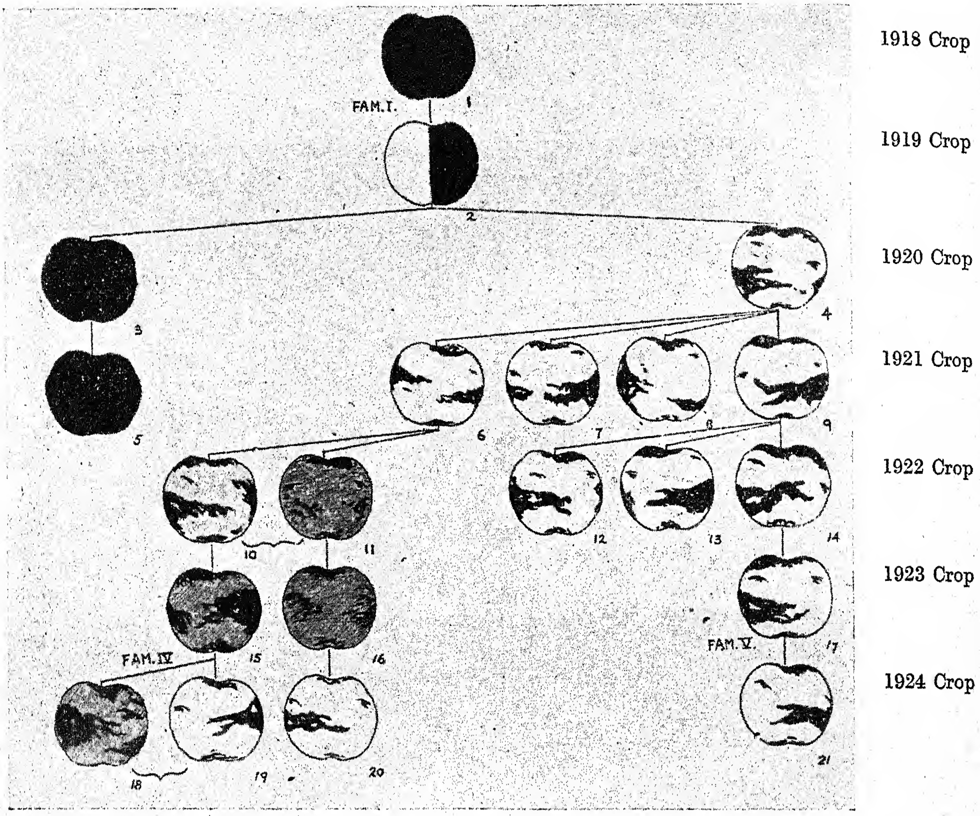

Fig. 1. McKelvie's Mutation No. 1.

Mutation A.V.V. 11, 12=*No.* 1 *of McKelvie.* Designed to show the different clones grown and the pigmentary character of their crops. The shapes are diagrammatic.

No. 1. Arran Victory, normal, self-coloured, deep blackish purple.

No. 2. The "Mutation" discovered by Mr McKelvie in 1919 and described as being half purple, half white, the division between the two being longitudinal.

No. 3. Normal self-coloured tubers, of which there were 36, derived by Mr McKelvie from No. 2.

No. 4. Parti-coloured, "splashed," purple tubers, five in number, derived by Mr McKelvie from No. 2.

No. 5. Normal self-coloured tuber derived from No. 3 by Mr McKelvie.

Nos. 6, 7, 8 and 9. Parti-coloured tubers derived from No. 4, of which there is no information as to whether the intervening areas between the purple "splashes" are white, or coloured a dilute purple or pink. All were grown in Scotland by Mr McKelvie.

Nos. 10 and 11. Tubers from the same parent No. 6, sent to R.N.S. by Mr McKelvie. The one, No. 10, has no pigment between the patches; the other, No. 11, has such.

No. 12. A parti-coloured tuber derived from Mr McKelvie's No. 9 seen at Ormskirk by R.N.S.

the Conference as if it were "splashed," *i.e.* the colour is shown as irregularly distributed in blotches. As a matter of fact the tuber was clearly divided into two halves: a coloured, and a colourless. It was planted whole.

The progress of events is displayed in Text-fig. 1. It will be seen that this aberrant tuber gave rise in 1920 to some fully coloured tubers typical of Arran Victory, and also to others which may be described as "splashed." From these latter, by direct descent, we reach No. 14, which represents the tuber sent to me as illustrating Mutation No. 1. This gave rise to plants successively in 1923 and 1924, all of which bore parti-coloured, "splashed" tubers in which the areas between the purple markings were colourless or white (see Fig. 4, Pl. VI). Mr McKelvie also sent me tubers Nos. 10 and 11, sister tubers from the same plant (Text-fig. 1, Nos. 10 and 11) which in its turn was derived from the original mutation. One of these tubers, No. 11, differed from the remainder by the presence of a suffusion of pinkish purple between the less well-defined and smaller dark "splashes": it was, in fact, less removed from the self-coloured parent variety than were the others (Fig. 3, Pl. VI). In 1922 this tuber reproduced its like, but No. 10 reproduced tubers similar to No. 11. In the following year, the tuber No. 16, with pinkish purple pigment in the intervening areas gave rise to a plant with nine tubers all "splashed," but free of pigment between the "splashes," whilst No. 15, itself furnished with suffused pigmentation between the "splashes," gave rise to plants bearing fourteen tubers like the parent and three others free of colour between the "splashes." The type of tuber coloration exhibited by No. 15 will be referred to as Mutation 1 A.

It will be seen that the colour changes do not proceed in a strictly ordered manner but show some evidence of reversibility. Full-coloured

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No. 13. A similar tuber seen at East Craigs by R.N.S.

No. 14. A parti-coloured tuber with no pigment between the patches, sent by Mr McKelvie to R.N.S. and planted in Barley.

Nos. 15 and 16. Parti-coloured tubers with dilute purple pigment between the patches, raised in Barley by R.N.S. from Nos. 10 and 11 respectively. No. 15 is the ♀ parent of Family $\frac{331}{24}$. In these two tubers there is a pinkish purple coloration between the "splashes."

No. 17. Parti-coloured tuber with no colour between the purple patches. Raised in Barley. No. 17 is the ♀ parent of Family $\frac{320}{24}$.

Nos. 18 and 19. Parti-coloured tubers, the one with, and the other without pigment between the patches. Raised in Barley from No. 15.

No. 20. A parti-coloured tuber without pigment between the purple patches. Raised in Barley and derived from No. 16.

No. 21. A parti-coloured tuber without pigment between the purple patches. Raised in Barley and derived from No. 17.

ARRAN VICTORY. MUTATION No. 13.

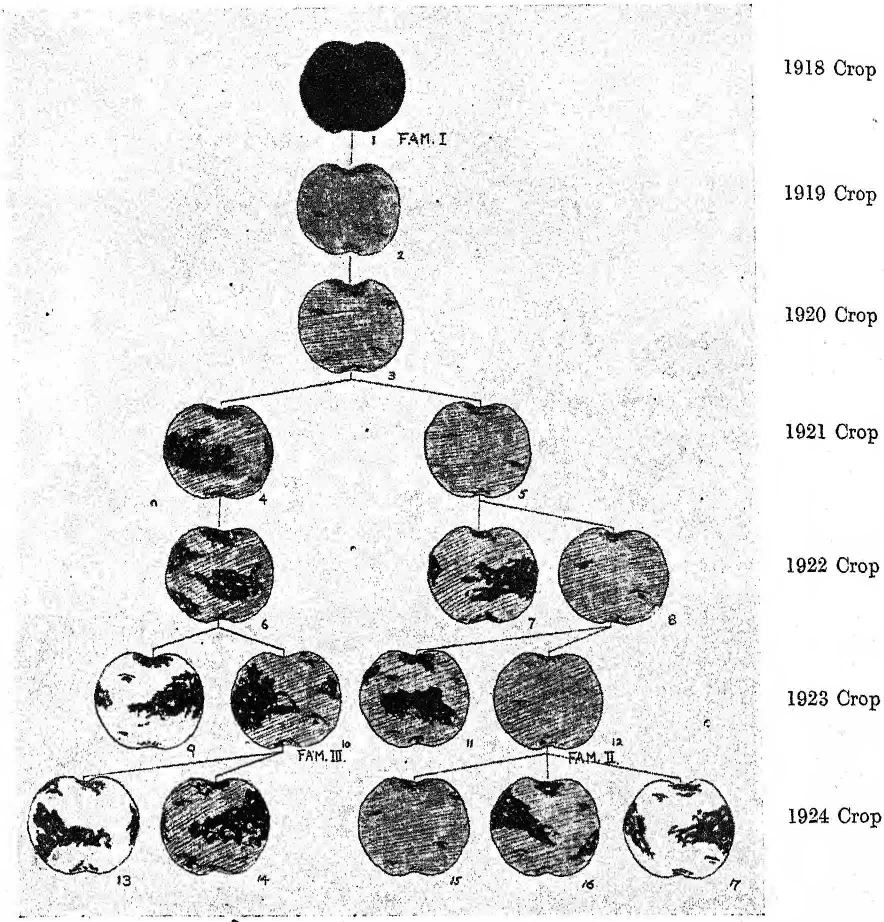

Fig. 2. McKelvie's Mutation No. 2.

Mutation A.V.V. 15 = No. 2 *of McKelvie.*

No. 1. Arran Victory. Normal, self-coloured, deep blackish purple.

No. 2. Mutation found in 1919 by Mr McKelvie and described as Mutation No. 2. The tuber is self-coloured dilute reddish purple with deeper purple at heel end and purple eyes.

No. 3. Similar to No. 2.

No. 4. A descendant of No. 3 described by Mr McKelvie as showing some deeper purple patches.

No. 5. A sister tuber to No. 4 similar to the parent tuber No. 3.

No. 6. Tuber similar in colouring to its parent No. 4, and sent to R.N.S. by Mr McKelvie.

Nos. 7 and 8. Sister tubers sent to R.N.S. the majority of which, like No. 8, were of the

tubers were obtained in 1920, according to Mr McKelvie, from the "splashed" mutant of 1919 but were not met with again, whilst I observed both the appearance and disappearance in the same "clone" of pigmentation between the "splashes."

Throughout, the eyes of the tubers in this mutation are all pigmented, and the "brow" above the eye also. The sprouts as grown in subdued light were all deeply purple and quite similar to those of Arran Victory.

The flesh colour in all was a very pale yellow, as is found in Arran Victory, and in many tubers a faint purple coloration was found in the vascular bundles, a feature common to the parent variety. It will be best to postpone the consideration of the tuber shape until the three mutations have been described.

The general appearance, as well as the more minute characteristics of the haulm of this mutation in the examples grown at Barley were alike and at the same time identical in all respects with those of Arran Victory. No difference in the degree of pigmentation of the skin, in the Leaf Index (6) nor in any of the finer details of the flower were observed.

In all, three lines of this mutation were under observation and are designated Mutation No. 1 (A.V.V. 12), Text-fig. 1, Nos. 14, 17, 21; No. 1 A (A.V.V. 12, "4 tubers"), Text-fig. 1, Nos. 10, 15, 18, 19; No. 1 B (A.V.V. 12, "3 tubers"), Text-fig. 1, Nos. 11, 16, 20.

There is no recognisable distinction between the two clones 1 A and 1 B. They are only distinguished here because they formed distinct material for observation and experiment.

Mutation 2. This arose from a tuber found in a "pit" of Arran Victory, the skin of which, instead of being dark purple all over, was in general of a pinkish purple colour; the eyes were the normal dark purple, and there was a small purple patch at the heel end (see Fig. 2, Pl. VI). The further development of this mutation is shown in Text-fig. 2.

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parent No. 2 type, being self-coloured pinkish red, or faint purple, with coloured eyes. The others, like No. 7, purple "splashed" with pinkish purple intervening.

Nos. 9 and 10. Parti-coloured tubers, one with, and the other without intervening coloration, derived from No. 6, and raised in Barley. No. 10 is the ♀ parent of Family $\frac{3.8.2}{2\,4}$ and is the representative of the clone Mutation 2 A.

Nos. 11 and 12. Offspring of No. 8, raised in Barley. One with deeper patches of colour, the other without. Both self-coloured purplish red. No. 12 is the ♀ parent of Family $\frac{3.8.3}{2\,4}$ and is the representative of the clone Mutation 2.

Nos. 13 and 14. Are parti-coloured tubers, the one with, the other without pigment in the area between the purple "splashes." Grown in Barley and derived from No. 10.

Nos. 15, 16 and 17. Are all derived from No. 12 and raised in Barley. No. 15 is self-coloured purplish red. No. 16 is similar but marked by "splashes" of deeper purple pigment, whilst No. 17 is parti-coloured and has no pigment in the intervening areas. The eyes and brows in all the tubers of this "line" are deeply pigmented.

Tubers were sent to me by Mr McKelvie in the spring of 1923 and the variations shown in the crops of 1923 and 1924 were personally observed.

The main difference to-day between this mutation and the one previously described is that whilst some tubers are more or less evenly pigmented, cf. Text-fig. 2, No. 15, the majority are "splashed," and between the dark purple splashes occur, as in Mutation No. 1 A, a suffusion of pinkish purple. Such a tuber is represented in Fig. 3, Pl. VI. Some tubers may differ from Mutation No. 1 A in that the purple coloration between the splashes is more concentrated than is general in these latter.

Both in 1923 and in 1924 a small percentage of the tubers derived from No. 2 Mutation plants were found which were in all respects similar to Mutation No. 1, *i.e.* there was no colour between the "splashes."

In this series, as in those of Mutations Nos. 1 and 1 A, the eyes are all deeply coloured purple, the shoots are a deep purple similar to those of Arran Victory, the flesh is again very pale yellow and, in most of the tubers of this mutation, there is present in the majority of tubers a little, but often enough a very considerable amount, of reddish purple coloration of the flesh commencing in the vascular bundles and spreading from thence to the medulla and, to a lesser extent, to the cortex. Two lines or strains of this mutation were sent me by Mr McKelvie who noticed, as I have done, that as regards the development of colour in the flesh, they differ. One, which we may call Mutation No. 2, represented by A.V.V. 15–3, and springing from the tuber represented by No. 8, Text-fig. 2, has but a trace of colour inside; the other, Mutation No. 2 A, which takes its origin from the tuber represented by No. 6, Text-fig. 2, has abundant colour inside. The two lines differ also as regards the occurrence of self-coloration as distinct from "splashing." In the one (A.V.V. 15–1) splashed forms only occur; in the other (A.V.V. 15–3), both splashed tubers and self-coloured diluted purple ones. In 1924 a count was made of the different types of coloration in the tubers harvested from each of these lines.

TABLE I.

	Self-coloured dilute reddish purple	Splashed with dilute reddish purple between	Splashed without intervening pigmentation
Mutation No. 2 A (A.V.V. 15–1). Descended from No. 6, Text-fig. 2	0	12	3
Mutation No. 2 (A.V.V. 15–3). Descended from No. 8, Text-fig. 2	8	2	2

The eyes and their brows are coloured a deep purple in all forms of this mutation.

The relative stability of Mutation No. 2, so far as the extent of the pigmentary loss is concerned, is well shown in the series as a whole. In some plants, the self-coloration peculiar to Arran Victory is maintained, but the purple pigment itself has lost much of its blue character and is consequently redder and more dilute in tone. In others occur tubers which are "splashed" but retain the self-coloration, whilst these latter have in turn formed plants which bore tubers some of which were themselves similar to the parent tuber and others indistinguishable from Mutation No. 1. It is noteworthy that the fully coloured Arran Victory type has not reappeared in this "clone."

The haulms of the plants included under Mutation No. 2 are in all respects similar to those of No. 1 and, like them, indistinguishable from those of Arran Victory.

In the flower buds of this mutation there was noticed in 1923 some purple coloration on the under side of the petal on either side of the median vascular bundle. This fades away later when the flower opens. No similar coloration was observed in any of the other mutations or in the parent variety. Unfortunately, no observation was made on this character in 1924.

Mutation 3 (A.V.V. 11). This was discovered by Mr McKelvie in a "pit" of Arran Victory. The original tuber was more or less particoloured, *i.e.* the heel end was purple "splashed," but the remainder of the tuber was colourless except for the eyes, all of which were pigmented. This tuber, oval in shape, sown in 1919, produced a plant with a typical Arran Victory haulm. Tubers similar to the parent type have been carried on by Mr McKelvie at Arran and have retained the original type as found in 1919. The amount of pigmentation, however, is rather variable, in some approaching a degree not far removed from Mutation 1, and in others nearing vanishing point. The tubers were of two kinds: some like the parent, No. 3, Text-fig. 3, others devoid of all colour, No. 4. The all-white tubers produced plants which bore tubers, some quite colourless, others marked with small patches of purple between the eyes. Examination of all the tubers of the 1924 crop showed that these "white" tubers were of various kinds: on some, no colour whatever could be found, on others an "eye" or "eyebrow" would be pigmented. In others, again, would be found a small patch of pigment quite unrelated to the "eyes." Mr McKelvie has selected several tubers from the "line" or "clone" on which small patches of pigment developed and has

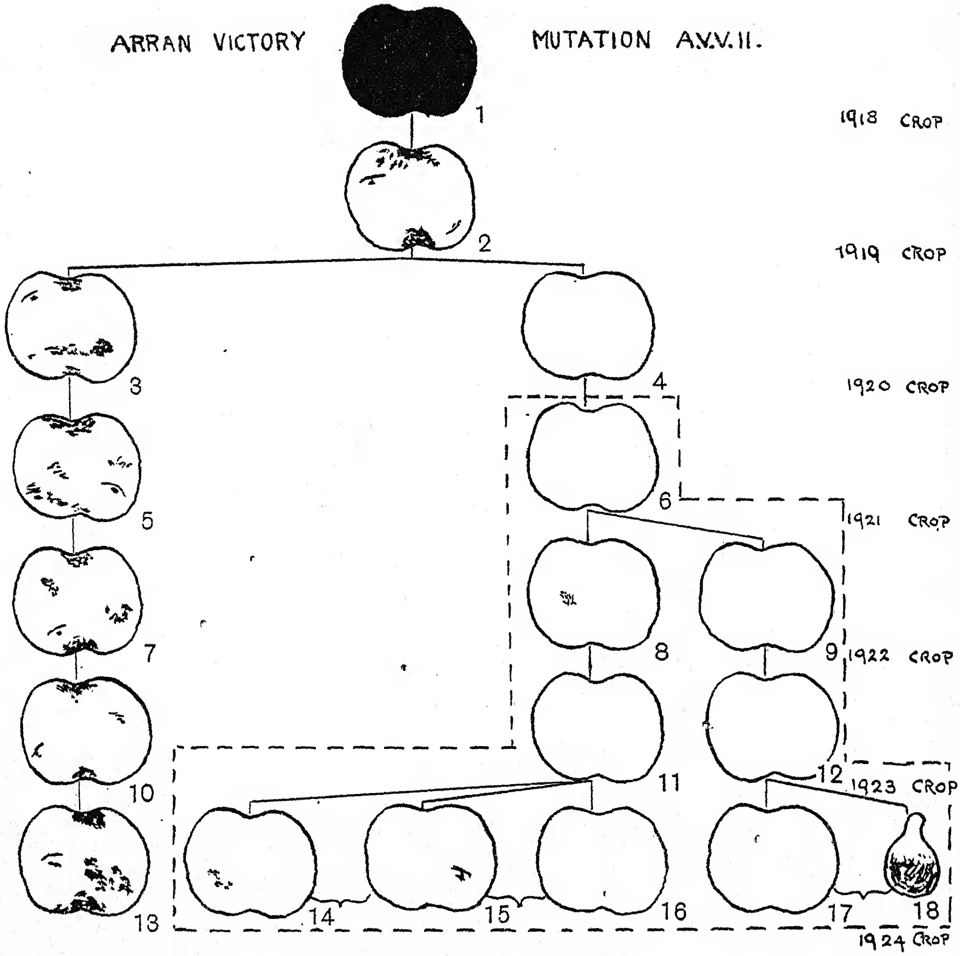

Fig. 3. McKelvie's Mutation No. 3.

Mutation A.V.V. 11 = No. 3 of McKelvie.

No. 1. Is a normal self-coloured blackish purple tuber of Arran Victory.

No. 2. A white tuber with a purple coloration at heel and crown with small spots of colour radiating from heel, and coloration in some of the eyes and brows.

Nos. 3, 5, 7, 10, 13. Are all descendants of No. 2, showing various degrees of coloration on a white background. All were grown by Mr McKelvie in Scotland.

No. 4. A pure white tuber derived from No. 2.

No. 6. Descendant of No. 4.

No. 8. Descendant of No. 6 in which a trace of colour has reappeared. Representing the clone Mutation 3 A.

No. 9. Fellow tuber to No. 8 with no colour. Both Nos. 8 and 9 were sent by Mr McKelvie to Barley in the spring of 1923, as representing the "clone" Mutation 3.

No. 11. Colourless offspring from No. 8.

No. 12. Descendant from No. 9, with no development of colour.

Nos. 14, 15 and 16. Descended from No. 11. The majority show no colour, the remainder show slight deposits, some about the eye, some outside it.

Nos. 17 and 18. Descended from No. 12. Of 31 tubers one (No. 18) that was exposed and abnormal, developed colour: the rest were colourless.

Nos. 11, 12, 14, 15, 16, 17, 18, were grown in Barley.

All those crops included within the dotted line showed the variation of foliage described in the text.

obtained some in which the patch has attained a considerable size amounting to what in Mutation 1 would constitute one of the main "splashes."

As is shown in Text-fig. 3, two strains have been kept separate: one derived from No. 9 (A.V.V. 11 A 6), which will be referred to as Mutation No. 3, produced no tuber with any colour in 1924 except for one exposed abnormal one. The other, Mutation No. 3 A, Fig. 5, Pl. VI, descended from No. 8 (A.V.V. 11 A 3) gave the two varieties of tuber already referred to, although the completely colourless ones were in the majority. The distribution of these tubers in the 1924 crop is shown below:

TABLE II.

		Tubers exhibiting some trace of purple colour				
	Colourless tubers	In the eyes only	In the brow of the eye only	At the heel end only	In a wound scar only	In the tuber side
Mutation No. 3 A (A.V.V. 11 A 3)	40	1	6	2	2	2
Mutation No. 3 (A.V.V. 11 A 6)	30	0	0	0	0	1*

* This tuber lay above ground and was exposed to the light.

Mutations Nos. 3 and 3 A, however, differ very widely from both No. 1 and No. 2, in that in the case of these latter the loss of pigment in the tuber is unaccompanied by any change in the haulm, whereas in both Mutations Nos. 3 and 3 A this is no longer the case.

Mr McKelvie noticed in 1921 that the plants which sprang from the pure white tubers, Text-fig. 3, No. 4, and all its successors differed from their immediate tuber parent plant as well as from Arran Victory itself, whilst those plants which arose from the original mutation, No. 2, and those others which arose in their turn from No. 3 and its successors were true to the Arran Victory type. The differences exhibited by the plants which arose from tuber No. 4 are to be found in all its descendants that are included within the broken line in Text-fig. 3. The haulms are shorter, the pigment common to the stem in Arran Victory and Mutations 1 and 2 is either minimal as in the plant represented as No. 11 in Text-fig. 3 or it is absent altogether, as in that shown as No. 10.

The most characteristic difference is, however, seen in the leaflets which in Mutation No. 3, whilst preserving the large size and general character of the type, are much narrower than those of the other mutations and of Arran Victory itself. The Leaf Index (6) of Mutation No. 3 is 50, that of Mutations 1 and 2 and Arran Victory is 61. A difference of

11 points is a striking one, as may be gauged by the comparison of the outlines of the two leaflets in Text-fig. 4. In the Potato Leaf between each pair of leaflets there occur intermediate leaflets known as folioles; these vary both in size and in number in different varieties. In the Type plant, as also in both Mutations 1 and 2, these folioles reach a very considerable development both as regards size and number. In Mutation No. 3 they are markedly smaller and generally fewer.

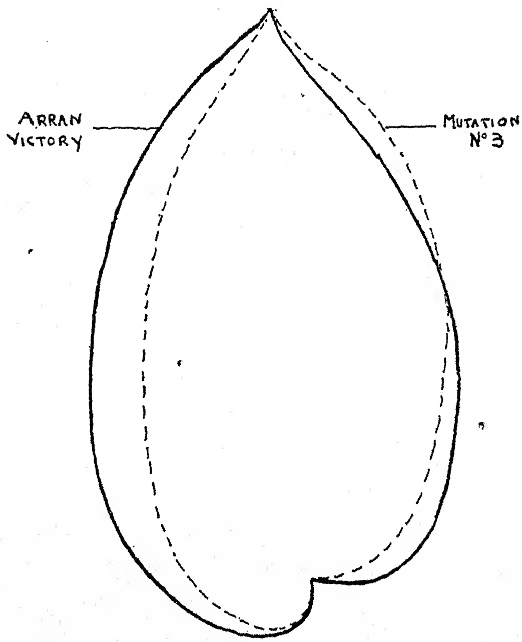

Fig. 4. Outlines of leaflets of Arran Victory and Mutation No. 3 representing the average Leaf Indices, 61 and 50 respectively, of each.

It has already been noted that there is little or no colour developed in the stem of the Nos. 3 and 3 A Mutations. The same absence of colour is to be observed in the midribs of the leaf which, in conjunction with a paler green tone of the foliage, creates a very distinct and striking difference between Mutation No. 3 and both Arran Victory and the two other mutations when they are grown in apposition to each other.

One has so far emphasised the differences between the Mutations Nos. 3 and 3 A and the type, but it is none the less essential to point out the likenesses. In their physiological characters there is no difference. Mutations Nos. 3 and 3 A are, like Arran Victory, of late maturity, and immune to Wart Disease. Their susceptibility to *Phytophthora*

infestans is also the same. In morphological characters the upright habit of growth and the crinkling of the wing of the stem is common to these mutations as it is to the others and to Arran Victory.

The flowers of both Mutations Nos. 3 and 3 A are identical with that of Arran Victory. It might be thought that as both are white, this fact in itself does not constitute any very weighty evidence of relationship. This view, however, is hardly correct because the flower of Arran Victory is by no means a common type: the corolla is small, the white of which has a yellowish tone; the anthers are strikingly long, thin, ill-developed, and most commonly irregular and they never contain any normal pollen, the five anthers form a long, narrow cone, pale yellow in colour; the style is of medium length, or sometimes short, and is slightly notched. In Arran Victory the flowers are fleeting and drop, some before opening and all very soon afterwards. All these characteristics are reproduced exactly in Mutation No. 3.

The identity of floral and other structures between Mutation No. 3 and the type should be borne in mind together with other evidence which will be adduced later, when the argument is put forward that this particular mutation of McKelvie's is not a genuine one but in reality is nothing more than a "rogue" which has accidentally crept into his cultures. My own views, based on the work here recorded, are entirely opposed to this suggestion.

All these mutations have been tested for susceptibility to Wart Disease and have proved themselves, like their prototype, immune. There is no evidence indeed of any change of a purely physiological nature other than an indication of a lessened genetic cropping capacity in the less pigmented mutations, which will be considered later. Mr McKelvie in his paper quotes some observations communicated by Professor Quanjer on a variety Leeland Blue by Mr Van Luyd, in which a blue round potato produced a number of colour mutants one of which was said to offer a greater resistance to *Phytophthora* than the type plant. Reports have reached me this year that the variety Field Marshal, which is an Up-to-date plant in every character except for a russeted skin to the tuber, is showing a greater resistance also to *Phytophthora* than is Up-to-date—itself one of the most susceptible of plants. The evidence in either case is vague and certainly not convincing, but there would seem to be no *a priori* reason for refusing to believe that a loss of factors affecting pigment production might have a secondary effect on such physiological processes as disease resistance, although there is no evidence of any such change in the mutations under consideration.

Tuber Shape in Arran Victory and its Mutational Forms.

It has been shown that genetically the shape of the tuber is essentially controlled by a pair of factors influencing the length of the axis, that for long axis being dominant (7). The recessive short tuber, or "round" is normally of a very characteristic shape, being short and thick, with a marked depression at the heel, associated with well-developed lateral shoulders, see Text-fig. 5, A. The crown or distal collection of buds is also very often depressed, and is generally not developed strictly opposite the proximal or heel end but is obliquely placed so that it occupies part of one lateral surface as well. Other shapes, described as ovals, kidneys and longs, are recognised in the industry. Actually the shapes most commonly met with amongst potatoes of all sorts may be grouped into eight classes. These are represented in Text-fig. 5, A–H.

I had long since realised that the typical apple-like "round" was subject to variations, the chief of which are represented in Text-fig. 5 as B and C. The "B" type is the most common, and such tubers may very readily deceive the unwary and be classed as longs. If they be, however, regrown, as has been very frequently done in Barley, the resultant crop will again reproduce the "A" type, often to the exclusion of both "B" and "C" types. The "B" type is characterised by being as broad or even broader at the heel than at the crown end, whilst the "C" type is narrower at the heel than at the crown end. This latter also faithfully reproduces the "A" as well as the "B" and "C" types when regrown. The essentially characteristic feature in both is the depression at the heel. The crown group of eyes is also depressed and, as in the typical round, is obliquely placed.

The "D" type, Text-fig. 5, differs from the true round by not exhibiting the depression at the heel end. Such types are rather rare and they are probably to be regarded as malformations of the "A" type and of no genetic interest.

The "E" type of tuber may be and probably is a modification of a round, but it is a very definite one; the elongation of the tuber is accompanied by a complete loss of the characteristic depression at the heel end. A tuber of this type occurring in a genetically pure family of red rounds in 1923 gave rise to a plant bearing true rounds only. On the other hand, this shape may not infrequently be found amongst a collection of kidney-shaped tubers, heterozygous for length.

The "F" type is the well-known "kidney" shape. The characteristics of such tubers are the oval ends, showing no depression at either

extreme, the strictly terminal position of the crown eyes and the even elliptical outline. The types "B" and "C" may approximate to the "F" type but there is not that clumsiness about the latter which is never absent from the "B" and "C" types.

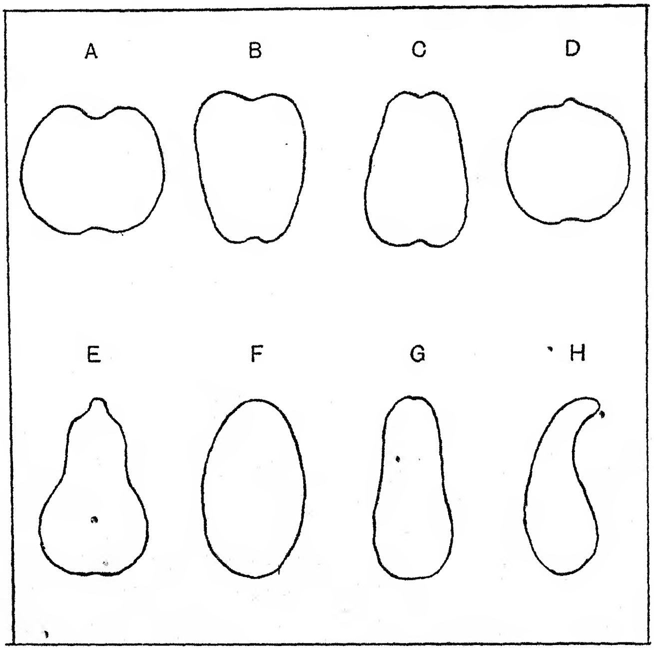

Fig. 5. Tuber Shapes.

A. Typical round, showing the depression at either end and the shouldering at the heel. Such a tuber is homozygous for the recessive factor, short axis.
B. Modification of "A"; a very common variant form in which the depression at either end persists. The tuber is lengthened but the heel end is broader than the crown end.
C. Modification of "A," a form which is common but less so than "B," from which it differs by being broader at the crown end. Both "B" and "C" are peculiarly thick.
D. An abnormal form of "A" in which the heel end is raised instead of being depressed.
E. An unusual form; sometimes occurring as an undoubted variant of "A." More often it is a variant of "F" or "G," characterised by the drawing out of the heel end.
F. Kidney shape; generally heterozygous for length. It shows no depression at either end and is less thick than "B" or "C."
G. Long; generally homozygous for length. In general, such tubers are cylindrical and blunt at both ends.
H. Finger-shaped; always homozygous for length. Breeds true by seed to the peculiar sickle-shaped heel end as well as reproducing itself by tuber propagation.

The "G" type is the long finger-shaped tubers which are found normally in such a variety as Myatt's Ashleaf. In a previous communication (7) it has been shown that type "F" is the normal shape of the

hybrid long × round. The pure dominant long is represented by the "G" type, though it often closely resembles the kidney or "F" type. The shape represented as type "H" is always pure for "length," but is in possession of some modifying factor which induces the tapering and bending over of the heel end. In commerce, varieties such as Salad Horn, and Bohemian Pearl are examples of type "H."

It may be said with confidence that the types "A"–"D" inclusive are but variations more or less common of the recessive round, and that "F", "G" and "H" are the shapes assumed by hybrids and homozygous longs respectively. This of course does not for a moment exclude the possibility that some further factor may not so influence a "round" as to make it appear as one of the "E"–"G" types and, conversely, that a true long might not be transformed into one or other of the "A"–"D" types of tuber shapes, by the action of some factor even in the presence of that for "long" when homozygous.

Arran Victory itself is a round, but like many round varieties the tubers vary very considerably in the direction of the long axis, so that they become more or less oval.

To determine whether any constitutional change as to shape is taking place in a variety it is advisable to analyse the crop in regard to these characteristics and to compare the tuber shapes over at least two consecutive seasons. This has been done, in respect to both Arran Victory and its mutations. In 1923 the variant types of tuber shape were described and figured, but the frequency only estimated. In 1924, however, a careful analysis of each has been made. Although one cannot make an accurate numerical comparison of the 1923 and 1924 results, it is at once clear from a study of the notes and drawings of the 1923 crop that there existed then an exactly parallel series of events to those of 1924. Only the forms which were found in the 1923 crop of each mutation occur in the corresponding crops of 1924. An analysis of the latter is given below. It will be seen that three lines of Mutation No. 1 and two each of Mutations Nos. 2 and 3 have been under examination. The differences between the strains of each separate mutation lay originally in a greater or lesser pigmentation and their origin is indicated in Text-figs. 1–3. The composition of the crops in respect to colour is shown in the right-hand column. The various mutations and their strains are placed in a descending order corresponding to the decreasing pigmentation exhibited in the tubers borne by them.

The analysis shows that Arran Victory and its Mutations Nos. 2 and 3 with their sub-lines bear tubers all of which are included in the types

TABLE III.

Name	Tuber shape types A %	B %	C %	D %	E %	F %	G %	Total No. of tubers examined	Description of pigmentation
Arran Victory	53	35	12	—	—	—	—	73	Deep purple distributed all over the tuber.
Mutation 2 A	73	27	—	—	—	—	—	15	Tubers all "splashed," some with dilute purple between the "splashes" and some without. The tuber flesh is freely pigmented.
Mutation 2	73	7	20	—	—	—	—	12	Dilute pinkish purple distributed all over the tuber with some deeper purple at heel and eyes. Splashed tubers, some with dilute purple between the "splashes," and some without.
Mutation 1 A	77	23	—	—	—	—	—	17	All tubers "splashed," majority with dilute purple between the "splashes," others without.
Mutation 1 B	77	23	—	—	—	—	—	9	All "splashed." Markings are smaller than above and no intervening pigmentation.
Mutation 1	80	20	—	—	—	—	—	14	All similar to above. The markings are rather larger.
Mutation 3A	47	17	—	—	21	—	15	53	Majority of tubers entirely colourless. Remainder with a spot of colour on brow of eye or elsewhere.
	$\underbrace{\quad}_{(64)}$					$\underbrace{\quad}_{(36)}$			
Mutation 3	13	16	—	16	—	35	20	31	All tubers entirely devoid of colour excepting one exposed to light above the soil.
	$\underbrace{\quad}_{(29)}$					$\underbrace{\quad}_{(71)}$			

"A," "B" and "C" and may therefore all be considered as "rounds" or temporary modifications of the same.

With Mutation No. 3 a change occurs. Of the 83 tubers examined 43 per cent. fall into the groups "E," "F" and "G." If we examine individually the tubers of the strain which does not develop any colour in its tubers at all, the proportion of "E"–"G" types is 71 per cent., whilst in the other line, No. 3 A, where minute patches do occur, it is only 36 per cent. Striking as the changes were as observed by myself in Barley, that exhibited by the tubers of this mutation grown in Arran is even more so. The entirely colourless "clone" Mutation 3 is phenotypically "long" as judged by the Scotch grown tubers.

We have already seen that Mutation No. 3 was characterised by more than a mere loss of pigment in the tuber and that, unlike Mutations Nos. 1 and 2, its foliage differed from the type stock of Arran Victory. Associated with, if not consequent on, the practically complete loss of

colour in the tuber, the Leaf Index was reduced so that the leaflet became long and narrow. A similar change is now seen to have overtaken the majority of the tubers.

It may be questioned whether this change of tuber shape is in essence the result of the modification of function or of a disturbance affecting the very existence of the short genes themselves, or whether it may not rather be due to a modification of the normal influence on tuber shape exhibited by the short-long genes consequent on a disturbance of the balance between the various genes induced by the loss of the purple and other pigment factors. The heavy reduction in the number of pure rounds of the "A" type might be held to support this latter view, but the behaviour of the mutation when crossed, to be discussed in a later section of this paper, would rather seem to point to some definite change of the short-long genes.

We may conveniently sum up at this stage the position as regards the nature of the mutations so far as their morphological and physiological characters are concerned. Starting out from the full-coloured Arran Victory, there is a progressive loss of colour in which certain definite stages may be recognised. The first change is one of distribution. The self-colour gives place to a parti-coloration: "splashes" of pigment occur having the same full tone as in the parent type, but their size varies so that in one "clone" they may occupy from 50–75 per cent. of the tuber surface, in another 25–50 per cent., and in a third from 10–25 per cent. The "eyes" and "brows" retain their pigment in all these "splashed" forms. The next change is a disappearance of the "splashes" and concurrently, of the deposition of purple in the "eyes" and the "heels," leaving the "brows" of the tuber with a trace of pigment. This latter is followed by a stage when all colour in the tuber, except for an occasional small patch of pigment around a lenticel, disappears. Finally, this too may vanish and there is left a "clone" in which the tubers are entirely free from pigment. The loss of pigment is only associated with other recognisable changes when it has reached a certain degree, represented by Mutations 3 and 3 A, when suddenly we find it accompanied by changes in the coloration of the haulm, the shape of the leaflet, and the form of the tuber.

The second change is one affecting the pigment itself. The distribution remains the same, i.e. the pigment is spread uniformly over the tuber, as in Arran Victory, but the colour is different, having lost much of its "blue" character. Mutation No. 2, Fig. 2, Pl. VI, shows this change very clearly. The same condition is present in the splashed tuber repre-

sented in the clones II A and I A where, between the full purple splashes, a pinkish purple suffusion of colour is to be seen.

In Mutation 3 occurs the "clone" 3 A, in which a trace of pigment is produced in occasional tubers; wherever it is found it is bluish purple and of the same tone as in Arran Victory itself, never the pinkish blue of Mutation No. 2. It would appear, therefore, that we have to deal with two quite distinct phenomena, the one a mutation affecting distribution of such pigment as owes its existence to the "Blue" gene "B" which in the presence of a "Red" gene "R" gives rise to full purple. The consequence is "B" and "R" occur together on the tuber skin only in certain chosen places. The other is a mutation affecting the pigment gene itself and not its distribution. It may be regarded as one in which the factor "B" is either suppressed or so modified throughout the tuber skin area as to leave "R" freer to exhibit its special influence. The distribution remaining normal, the tuber now appears as red instead of purple, but is otherwise entirely similar to Arran Victory.

GENETIC ANALYSIS OF THE MUTATION.

All the three mutations were sterile on the male side, so that selfed families could not be obtained. In 1923 I crossed Arran Victory itself, and the three Mutations Nos. 1 and 1 A, Nos. 2 and 2 A, and No. 3, all by the same individual, a seedling of a much inbred line (133 B 16.24.18) which we may call "X." The seedling was a white tubered kidney variety, pure for tuber colour, or rather its absence, and white of flower, but heterozygous for tuber shape. The fertilisations and the subsequent raising of the seedlings were undertaken with the usual precautions. None of the six families were big, for neither Arran Victory nor its mutations were found to be particularly fertile on the female side.

An analysis of the families as regards colour is seen in Table IV. The numbers indicate the percentage of individuals in the families, the tubers of which are deep purple (black), red, or white (colourless), respectively.

TABLE IV.

Name	Family No. in 1924	Black %	Red %	White %	Total of seedlings
Arran Victory × "X"	378	37	21	42	38
Mutation 2 A ,,	382	35	50	15	20
,, 2 ,,	383	37	26	37	27
,, 1 A ,,	381	28	27	45	49
,, 1 ,,	380	8	15	77	13
,, 3 A ,,	379	—	—	100	13

The families are arranged in a descending order corresponding to the amount and depth of pigmentation present in the mother tuber.

The number of black (purple) tuber-bearing offspring is seen to occur in a descending order, parallel to the decreasing extent and tone of the pigment present in the parent tuber. But it is when we come to Mutation 1 and that form of it in which the splashes are small and there is no intervening reddish pigment that the drop in the percentage of "black" seedlings is really large. When we pass to the third mutation we find all the offspring are completely devoid of colour in every tuber. It is not known exactly which parent tuber in the Mutation No. 2 gave rise to the plant which was cross-pollinated; it is possible that it was one less strongly pigmented than those of this "clone," which are not only strongly splashed with deep purple but also suffused with a general pigmentation of reddish purple. On this supposition, it was thought to be more correct to place it below Mutation 2 A rather than above it. The sudden rise in this latter family in the percentage of red-tubered offspring recalls the fact that the parent exhibited a considerable quantity of red in the coloration between the patches and in the flesh colour. Seeing that red is recessive to purple; it is possible that we have some interference with the genes for purple leading to a transformation of the latter to a red producing factor; the numbers, however, are too small to be pressed far as evidence for this suggestion.

It has been noted that the fall in the percentage of black offspring becomes dramatic when the family whose mother is Mutation 1 is reached. The numbers are small, but even so there can be no mistaking their tendency, especially when one compares them with those of the Mutation 3 family, where the reduction of colour reaches its extreme limit. The parent tuber of Mutation 1 is much less pigmented than either 1 A or either of the parent lines of Mutation 2. This year it was estimated that the "splashed" areas in Mutation 1 did not occupy more than on an average 15 per cent. of the surface of the tuber, whereas the areas covered in Mutations 1 A and 2 A varied from 50 to 70 per cent. of the tuber surface.

It is obvious from the above results that we are not dealing with a simple Mendelian segregation. The obvious suggestion is that just as the pigmentation of the mutated tubers present a mosaic, so is there a mosaic amongst the ovules, a varying percentage in every plant bearing the genes for purple or red. It is greatly to be regretted that only 13 individuals of the 3rd Mutation family survived, but the fact that not a tuber in the whole series displayed any pigment is considerable evidence that we have here a family in which a coloured tubered plant would be rare. It will be recalled that in Mutation No. 3 there were two lines or

"clones," one in which some tubers presented an occasional trace of colour, and the other in which this did not occur. The family raised from the cross by "X" is mothered by a plant of the first series, though the actual tuber which gave rise to the mother plant was apparently devoid of any pigment. This tendency to a minimal deposition of pigment in the tuber would thus seem to be unrepresented in the germ cells of the plant.

A fact of much interest in relation to all the six families produced by the cross with the seedling "X" is that wherever coloured tubers occur they are invariably self-coloured. There is no trace whatever of the "splashing" so characteristic of the mutations.

The flower colour of the parent seedling "X," as well as that of those of the mutations, is white; in the mutant form No. 2, it will be remembered, some flowers showed a trace of purple on the under side of the corolla. In the six families, 76 plants bore blooms, all of which were white, whilst on many other plants such buds as showed any signs of developing were furnished with white corollas but dropped before opening. In all the families derived from the mutations a certain number of flowers displayed some purple coloration on the under surface of the petal. The proportion of this type of flower was remarkably constant, viz. about 70 per cent. The parent "X" had no colour on the under surface of the corolla.

The anther cones in Arran Victory and the mutants are long, narrow, pale and devoid of pollen. In the seedling "X" the anther cone is broader, orange-coloured and the pollen abundant. In the seedling families, half the flowers have the narrow anther without pollen and the other half broader ones with pollen. This is as would be expected if Arran Victory is heterozygous for sterility as has been shown by Salaman (4). The style of Arran Victory and of the mutant forms is either short, i.e. it scarcely protrudes above the apex of the anther cone, or it is in some flowers of medium length, i.e. it projects about 1/16th to 1/8th of an inch. The seedling "X" is furnished with a long style projecting freely beyond the anther cone 1/8th of an inch or more. The families of all the mutations and of Arran Victory show segregation in respect to this character. 50 per cent. are short or medium, 50 per cent. are long: the actual numbers are 35 : 33, from which it may be inferred that the short type is the dominant form and that in the heterozygous condition the style may vary from short to medium.

A further character of the style which was observed was the stigma, as to whether it was deeply notched or more or less smooth and round. The numbers here are variable, but in all the families there are some

plants with one type and some with another. It may be said that in all these mutations, as well as in Arran Victory, the types of flower occurring in the families raised from them are similar in all respects. This identity of the floral organ is further evidence of the genuineness of McKelvie's Nos. 3 and 3 A Mutations against which, as has already been stated, some objections have been raised.

The colour which develops in the stem of a potato plant, and is technically referred to as "bronzing," is always of a reddish purple tone, the varying intensity of which would seem to depend rather on the greater concentration of the pigment than any specific alteration of colour. This intensity of pigmentation is associated with a greater or less spread of the same over the stem. The following classes depending both on the localisation and on the tone of the colour may be recognised, and are represented in Pl. VII.

Stem colour No. 0. No pigment can be seen above ground, a few punctate deposits can generally be found below.

" No. 1. A trace of pigment at the lowest nodes or at the ground line, with an often faint development of the same between the lower nodes.

" No. 2. The pigment can be seen both between the nodes and more particularly on the nodes throughout the stem: it is always "mottled," i.e. laid down in small islets with pigment-free areas between.

" No. 3. The colour is considerably more concentrated, reaches throughout the entire stem, being more intense in the lower part. The deposition of the pigment is much more uniform than in No. 2, appearing to be practically continuous in parts of the stem.

" No. 4. The colour is so concentrated as to cause the stem to appear black: the coloured islets are in general so closely packed as to seem continuous over the entire surface of the stem.

The seedlings belonging to the various families derived from Arran Victory and the mutations by crossing with the seedling "X," whose own stem colour is "0," varied as to stem colour as is shown below:

TABLE V.

Parents				Seedlings				
					Stem colour			Total No. of plants examined
♀ parent	Stem colour	♂ parent	Stem colour	Family No.	No. 1 %	No. 2 %	No. 3 %	
Arran Victory	3	"X"	0	378	38	35	27	37
Mutation 2 A	2	"	0	382	37	52	11	19
" 2	2	"	0	383	15	63	22	27
" 1 A	2	"	0	381	44	39	17	48
" 1	2	"	0	380	43	57	0	14
" 3 A	1	"	0	379	77	15	8	13

The mother plants are arranged in a descending series as regards the quantity of pigment present in the tuber; the seedlings show a

rapidly increasing number of stems with the minimum quantity of pigment present. If the individual families of Mutations 1 and 2 respectively are combined, the effect is more striking. See Table VI.

TABLE VI.

Parents				Seedlings				
					Stem colour			
Name	Stem colour	Name	Stem colour	Family No.	No. 1 %	No. 2 %	No. 3 %	Total No. of plants examined
Arran Victory	3	"X"	0	378	38	35	27	37
Mutation 2	2	,,	0	382 & 383	24	59	17	46
,, 1	2	,,	0	380 & 381	43	43	14	62
,, 3 A	1	,,	0	379	77	15	8	13

There may be some difficulty in allocating a stem to No. 1 rather than to No. 2 class, or *vice versa*, but that is not so with regard to the No. 3 class. Such stem colorations are so definite as to allow of no hesitation in their classification. It is therefore a safer guide to note the decreasing percentages of the No. 3 class rather than the increasing one of No. 1.

It is interesting to observe that Mutation 3 does produce an occasional offspring with strikingly coloured stems, a fact which may be viewed as another link in the evidence proving that it is a genuine derivative from Arran Victory, and it suggests moreover, although only indirectly, that had the family been a bigger one, it might have contained a black-tubered seedling.

The shapes of the tubers of the seedling families are of interest. In an earlier part of this paper the range of variation from the normal round tuber which was displayed by the various mutant forms was discussed. Arran Victory and the Mutations 1 and 2 with their sub-lines all bore tubers, which were referred to shapes defined as A, B and C, common variations of the pure round. Mutation 3 bore a large percentage of tubers which were more elongated and fell for the most part into classes F and G. An analysis of the tuber shapes of the individual seedlings of the families derived from the crosses by seedling "X" is given in Table VII.

In this table, those individual plants whose tubers fall into groups A–C inclusive are classed as rounds, and those which fall into groups E–G as longs. There was no difficulty in separating the seedlings out on this basis.

Seedling "X" was evidently heterozygous for the length factor and

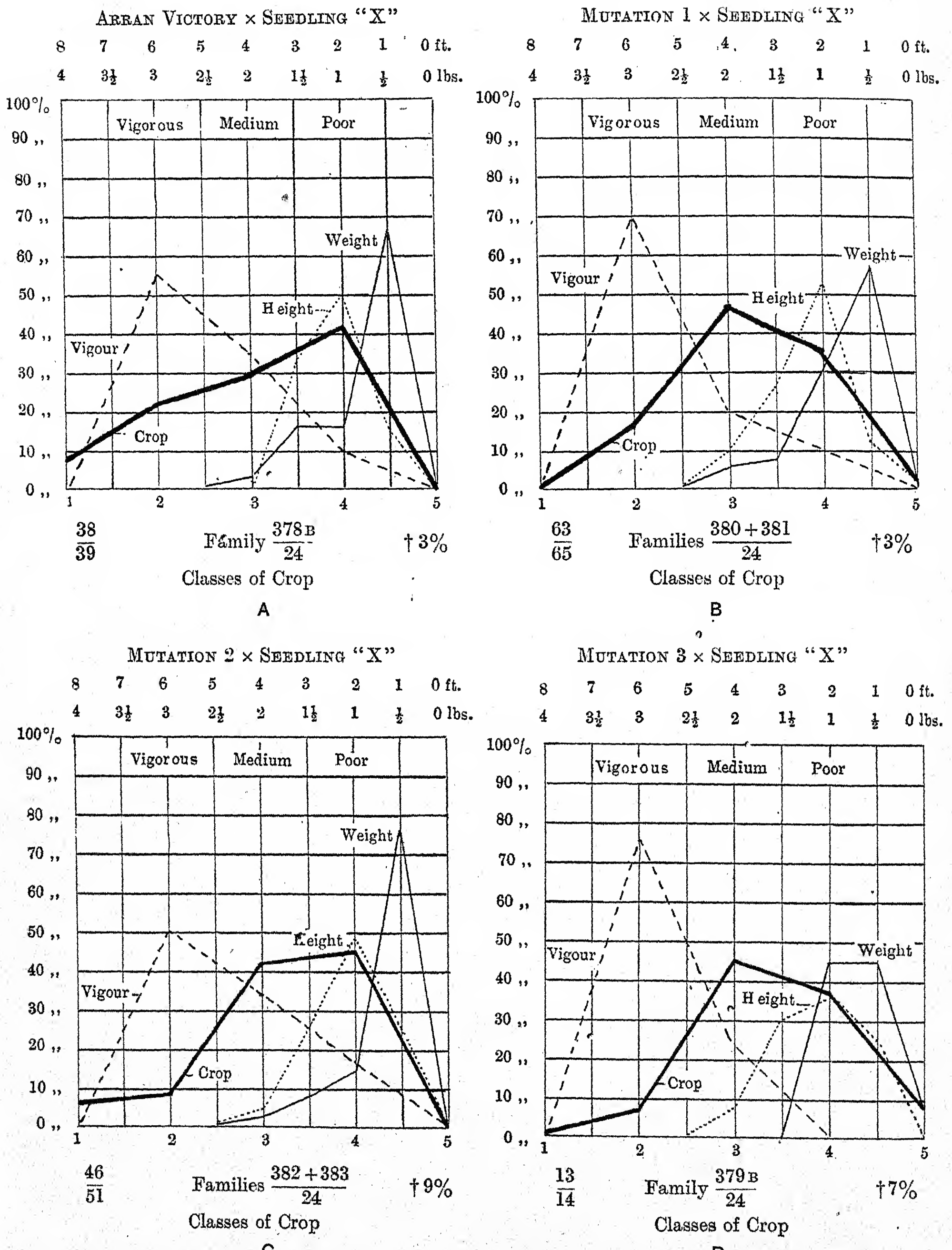

Fig. 6. Cropping Curves.

TABLE VII.

Name of family	Family No.	Rounds %	Longs %	No. of individuals examined	
Arran Victory	378	43	57	37	141
Mutation 2	383 & 382	45	55	45	
,, 1	380 & 381	48	52	59	
,, 3 A	379	17	83	12	

Arran Victory and Mutations 1 and 2 when mated with it give a ratio of rounds to longs all suggestive of 1 : 1. But all three throw less rounds than are to be expected. Grouping them together we have 141 seedlings of which 64 or 45 per cent. are round instead of 50 per cent. The standard deviation from a 1 : 1 ratio in this case is ·042 and the difference observed is rather more than this amount and almost twice the probable error. It cannot therefore be strictly considered as significant. With regard to the deviation shown by Mutation 3 from the expected ratio of 1 : 1, this amounts to 2·4 times the standard deviation or 3·5 times the probable error. Such a deviation as this is very unlikely to be due to chance, especially when it is considered in relation to the change of shape recorded in the parent tuber of the mutation. Viewed in the light of these facts, the lesser deviations of the other mutation families gain an added significance and suggest that some force is at work in the germ cells which brings about a progressive elongation of the seedling tubers, *pari passu* with the loss of pigmentation in the parent plants.

The actual and relative crop of the seedlings.

The actual crop. The average weight of tubers at each root with its probable error for the various families is shown in Table VIII.

In all the average crop must be regarded as a low one, indeed unusually so, for a first cross when grown at Barley. There is no outstanding difference between the average weight of a crop of any of these

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In these figures, the heavy continuous line represents the curve of relative cropping of the family of seedlings concerned; the light continuous line, the curve of the actual weights in ½ lb. intervals; the heavy broken line represents the incidence of vigorous, medium and poorly developed plants present in each family. The finely broken line represents the height of the plants in feet.

The numbers in the left-hand corner are as to the numerator the number of seedlings planted out, and as to the denominator the number which survived after the first week in August. The number following the sign † is the percentage mortality of each family.

Fig. A. Illustrates the curves for crop, weight, vigour and height of the seedlings derived from the cross Arran Victory by "X."

Fig. B. Represents a similar series of curves for the crosses of both Mutations 1 and 1 A combined, by "X."

Fig. C. Represents a similar series of curves for the crosses of both Mutations 2 and 2 A combined, by "X."

Fig. D. Represents a similar series of curves for the cross of Mutation 3 by "X."

TABLE VIII.

Family No.	Parents. Name of family	Seedlings: No. of seedlings	Average weight in lbs.	P.E.
378	Arran Victory × "X"	38	·63	±·35
382	Mutation 2 A ,,	19	·37	±·36
383	,, 2 ,,	27	·56	±·30
381	,, 1 A ,,	49	·63	±·34
380	,, 1 ,,	14	·69	±·27
379	,, 3 A ,,	13	·56	±·21

six families, and in each the probable error is so high that a difference would need to be about 1 lb. between any two averages in order to have any significance.

There is here then no evidence of any reaction on the offspring in regard to the weight of crop or the range of variation, resulting from the lesser pigmentation of the mutant mother plant.

The distribution of the plants through the families in respect to their weight can be seen in the curves on Text-fig. 6. For the purpose of these curves the crops are grouped in classes of ½ lb., 1 lb., 1½ lb., etc. and the finer differences are therefore lost sight of. Notwithstanding, the weight curves are all very similar as would be expected from the fact that the average crops, and the probable error of each, all range round much the same value.

Another method of estimating crop, and one giving us far more information with regard to genetic influences, is one I have already described in a preliminary paper (5). It is based on the estimation of the crop expressed as a relation between the size of the haulm of the plant and the tubers borne on it. In practice the plants forming a family are grouped in five different classes of relative merit as croppers, and a curve serves to record the result and characterise the fundamental cropping capacity of the parent plant or plants from which the family arose.

The curves thus derived from the three mutations and the original Arran Victory are shown in Text-fig. 6. The shape of these curves is extraordinarily similar: they are all alike very poor, or entirely deficient in first-class crops, but a comparison shows that the falling off in No. 1 and No. 2 crops (the classes containing the better crops) increases as we descend the series in the order of the colour of their parents—indeed in the last two we have examples of "zero croppers," i.e. well grown plants producing no crop. It is not necessary to discuss here the exact meaning to be attached to "zero croppers," but their occurrence in Mutations

1 and 3 together with the progressive loss in the crops of higher value can hardly be overlooked. If in the case of Mutation 3 the family is too small to allow of far-reaching deductions being drawn from the curve; the fact that it contains no representatives of Crop 1 but does contain a very excellent example of a zero cropper—a great lusty plant with no tubers—is a fact of more than passing interest. We have seen that the loss of pigmentation brought in its train both somatically in the tubers of the "clone" and genetically as shown in the seedling families a change of tuber shape. It would appear that a change of a definite character in the cropping capacity of the mutation, as shown by the cropping curves, also occurs as a sequence of, or at least in association with, the gradual loss of pigmentation in the parents.

Two other characteristics, vigour of growth and height of haulm, have been studied. Plants are classed as "vigorous," *i.e.* good strong substantial plants—a character which can be independent of mere height or size—"fair," *i.e.* plants of medium growth; and "poor," *i.e.* plants noticeably below the average in vigour of growth. The curves illustrating the distribution of the plants as regards this character are shown in Text-fig. 6. They all exhibit very much the same degree of vigour. As regards height, in all the mode is at 2 ft. and the range of variation very much alike in all. A comparison of the percentage of plants in each family attaining a height of 1, 2, 3 and 4 ft. respectively, gives a good idea of their general similarity in this respect and also tends to confirm the inference as to the similarity of their vigour.

TABLE IX.

The vigour and heights of the seedlings.

	Seedlings					
Parents. Name of Family	Vigorous %	Plants 1 ft. %	Plants 2 ft. %	Plants 3 ft. %	Plants 4 ft. %	No. of plants in family
Arran Victory × "X"	55	17	50	33	0	38
Mutation 2 ,,	50	23	47	26	5	46
,, 1 ,,	70	12	52	26	10	63
,, 3 A ,,	77	27	36	30	7	13

The incidence of Leaf Roll and Mosaic, as well as that of the Late Blight, amongst the seedlings within each family group was observed, notes were made several times during the season and the symptoms of Leaf Roll and Mosaic were recorded: occasionally both were present in the same plant: in these cases the plant is included under the more

serious infection and recorded again in the column set apart for mixed infection. The results are seen in the annexed table.

TABLE X.

Parents. Name of Family	Seedlings: Healthy %	Leaf Roll %	Mosaic %	Mixed infection %	No. of plants
Arran Victory × "X"	26	39	35	5	38
Mutation 2 ,,	32	28	40	4	47
,, 1 ,,	38	30	32	9	63
,, 3 A ,,	38	24	38	7	13

The incidence of each of the diseases, as well as the proportion of resistant plants in each family, present a very close similarity which, in view of the difficulty of the determination, and the consequent uncertainty in some instances of the diagnosis may be regarded as showing an almost perfect uniformity. It is thus clear that in regard to Virus Disease the mutations show no significant differences amongst each other as compared with the type. The inroads of ordinary blight (*Phytophthora infestans*) on the plants of the various families has been noted at harvest and an analysis of the results is shown in Table XI. Four grades of severity are recognised, which vary from a slight touch affecting one or two leaves to increasingly severer onslaughts culminating in grade 4, where the entire plant, leaves and stem, are heavily involved. In this series of seedlings there were none sufficiently severely attacked to be placed in grade 4. In this, as in the case of Virus Disease, there is no real distinction between the behaviour of the families derived from the type and those from the mutants. Similarly with maturity, the range of variation in ripening was the same for all. The seedlings have not been as yet tested for Wart Disease: it will be remembered, however, that all the mutants, like Arran Victory itself, were immune.

TABLE XI.

Parents. Name of Family	Seedlings. Degrees of *Phytophthora infestans* on the haulm at the time of harvesting: Healthy %	No. 1 %	No. 2 %	No. 3 %	No. of plants
Arran Victory × "X"	6	52	38	4	38
Mutation 2 A ,, / ,, 2 ,,	4	53	33	9	45
,, 1 A ,, / ,, 1 ,,	3	56	34	7	62
,, 3 A ,,	14	55	31	0	13

We may now consider the evidence the seedling families have provided in relation to the particular phenomena of somatic mutation which have been described in this paper. In the first place, it is clear that the changes which are evidenced in the somatic mutations, the gradual quantitative withdrawal of pigment more particularly, find their counterpart in the distribution of the cognate factors amongst the germ cells, *i.e.* the ovules. Again, whilst loss of pigment in the tuber is shown by a withdrawal of it from certain areas and its persistence in others, in the seedling families the pigment when present is evenly distributed throughout the whole surface and with an intensity generally no less than that seen in the original Arran Victory. We may picture this latter event as being due to the mating of an ovule in which the required genes for purple or red colour are present but in which there is no factor restricting its deposition, with a pollen grain which is conveying no purple (and probably no red) factor but which may contain a gene for "self" distribution of colour. Of course it might be assumed that the ovule was possessed of a recessive gene controlling some form of partial coloration, but for reasons which will appear later, this is not the most probable explanation in the present case.

The increasing scarcity of coloured tubered seedlings in the families as we descend the scale of mutations from which they arise, would point to the existence within the ovary of a mosaic of ovules, a varying number of which are charged with the genes of colour, and not to a decreasing efficiency to produce colour exhibited by the genes themselves, for if the latter were the case we should expect such coloured tubered seedlings as occur to be very dilute, whereas this is not the case, they being mostly as strongly coloured as Arran Victory.

It is of course a well recognised fact that a potato plant may be highly charged with colour in the stem and foliage, as for example the Champion, and yet bear white tubers, so that the production of colour in the tuber may be due to special genes, or alternatively, its absence due to inhibitors of colour, in either case with special localised function. In Mutation No. 3 the tubers have lost all or nearly all trace of colour, but the stem has done so to a much less extent. That one of the thirteen seedling plants derived from this mutation had a No. 3 coloured stem shows that the power to produce pigment in a concentrated form in the plant generally is not lost, even if it be so in regard to the tuber; the existence of colour in the lower surface of the petal in the bud stage of the flowers of the majority of the plants points to the same conclusion. Whether we are dealing with inhibitors preventing the deposition of

pigment in the tuber, except in certain spots, or with pigment genes P_1, P_2, P_3, etc., each producing colour in a special part of the tuber, would seem to be settled as against the former alternative by the fact that on crossing with "X," all the coloured tubered seedlings are self-coloured. Presumably a colour inhibitor must be dominant, and in these families it is self-coloration which is dominant, so that the inhibitor theory does not hold. It would then seem that what is happening is the loss of certain colour genes, more particularly such as assist in producing pigment in the tuber. One can picture this loss as occurring in a particular bud cell or cells in the tuber eye, and in consequence a greater or lesser number of the cells which spring from the bud area, to form a new plant with its new tubers are deficient in the requisite number of cells possessing the gene in question. Thus if we assume a P_y which causes purple pigment in the tuber, and P_x which does the same in the stem or rest of the plant, we might have some agency at work which destroyed P_y in 50 per cent. and P_x in only 25 per cent. of the cells of the bud. The consequence would be that some cells would contain P_y and P_x, others only P_y or P_x, and others neither. In this way Mutation 3 might arise from bud cells devoid of P_y, but containing P_x, perhaps in every third or fourth cell.

The possibility of a Purple-forming gene being transformed into a Red-forming one normally recessive to it, is suggested by the high percentage of red skinned offspring in the family borne by Mutation 2 A, as well as by the appearance of the parent tuber itself. Such a change might well be a stage in the progressive destruction of a multiallelomorphic locus.

This suggestion, however, does not explain the nature of the distribution of the pigment over the tuber surface of the mutations. Previous work, as yet unpublished, suggests that there are in some varieties special genes controlling pigment distribution in the tuber, and giving rise to complete coloration, patched or mottled coloration or colour limited to the eye, and that it is possible that these may be viewed as a series of multi-allelomorphs. Recently Collins (1) has made a similar suggestion in respect to the coloration of the King Edward VII variety. On this supposition changes in the gene for colour distribution would be represented by the following changes in the tuber. Self-distribution would pass to patching, patching to eye and brow coloration, eye and brow colour to brow colour alone, brow colour to occasional lateral patches.

It is possible to regard a tuber as a mosaic of cells, some containing

one, some another of these colour distribution factors, and this might account for such forms as those tubers in Mutation 2 where patching is combined with a weakly-developed self-coloration. The self-coloured offspring from the Mutation 2 would thus be due to the presence in the parent seedling "X" of the homozygous dominant gene for self-distribution of colour.

A rather simpler theory, and one which would accord with a large number of observations on colour in tubers is the following: In the cells which build up the periderm and the immediately underlying tissue of the tuber there may be different elective affinities as between the cells of one part and that of another on the one hand, and the pigment-producing cells on the other. Or the same idea might be expressed by regarding the different parts of the tuber periderm as endowed with metabolic activities in a descending scale and that each area attracts to itself pigment-producing cells in a corresponding order. Thus we might construct a gradient in which the highest point is represented by 1 and the lowest by 5 in the following scale:

1. A small area around the junction of the stolon and the tuber.
2. The "brows" of the "eyes," especially those near the crown end.
3. The "eyes," that is, the area within the depressed region containing the bud germs.
4. Patches, irregular in size, between the eyes.
5. Complete self-coloration.

When the "*Anlage*" of the tuber is being laid down in the bud, the areas would attract to themselves such pigment-producing cells as were present, in the order given, so that if there were not enough pigment cells to completely cover the tuber those patches only would show up, which were previously hidden under the "self" pattern, and associated with the patches would be either no colour intervening or an imperfect, *i.e.* less concentrated colour between the "patches" which would appear less purple and more pink.

That it is not the higher metabolic activity of certain tuber parts which itself produces an anthocyanin present potentially in every cell, is shown by the decreasing number of coloured seedlings in the families derived from the lesser coloured mutant form.

Both the occurrence, and the character of the somatic mutation would, on the view suggested above, be explained as being due to a progressive loss of cells containing the P_x, and probably the R_x genes necessary for purple and red pigmentation in the tuber buds: and the

actual distribution of the pigment as being determined by the special affinities or metabolic activities of different parts of the tuber respectively towards pigment-producing cells.

Neither suggestion, however, precludes the possibility of pattern genes in other varieties, for which there seems to be considerable evidence.

It is evident that loss of pigment in the tuber is not the sole effect produced by the disturbance which is occurring in the buds of these mutations. At a certain stage a perfectly definite alteration in the foliage appears, and a no less noticeable alteration in the tuber shapes: whether the former is conveyed to the seedlings was not ascertained, but that the latter is, is certain. In addition to these changes there is good reason to suspect that concurrently there occurs a lowering of the relative cropping capacity of the seedling offspring plants which is due to some interference with the genes which control directly or indirectly this function. If the whole phenomenon is primarily due to some alteration in the genes controlling colour formation in the tuber it is evident that these genes must at the same time be exercising other and far reaching effects on the constitution of the plant.

Summary.

Mr McKelvie's mutations of Arran Victory are characterised by increasingly greater losses of pigment in the tuber.

Up to a certain stage the other parts of the mutant plants do not vary from the type.

When the loss of pigment from the tuber is practically complete, a change takes place both in the haulm, and in the shape of the tuber.

Notwithstanding the loss of pigment, there still remain sufficient resemblances to confirm the relationship of this extreme mutant form with the type plant. There is no reason whatever to doubt but that McKelvie's Mutant No. 3 is derived from Arran Victory.

The type and all the mutants were crossed by the same domestic seedling; an analysis of the resultant families demonstrates that with the reduction of pigment in the tuber there is *pari passu* a reduction in the number of ovules capable of giving rise to coloured tubers.

Parallel with the reduction of coloured tubered offspring is a reduction of colour in the stems, following closely the decrease of pigment in the mutant mother tuber.

There is an excess of long-tubered seedlings in the family derived from the mutant which has lost most pigment.

There is some evidence that the heritable cropping capacity of the mutants is lowered with the loss of pigment in the tuber.

Both the type and all the mutant forms convey to their seedlings the same degree of susceptibility towards Leaf Roll and Mosaic as well as towards the attacks of *Phytophthora infestans*.

The somatic mutations of the tuber are, in this case, represented *pari-passu* by appropriate changes in the germ cells which are present in the ovaries of the plants which issue from such tubers.

A somatic mutation which is characterised by the loss of a specific character such as pigmentation of the tuber skin, may evince this loss in other directions both in its own body, and, through its germ cells, in its offspring.

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EXPLANATION OF PLATES VI AND VII.

Plate VI.

Fig. 1. A tuber of Arran Victory, normal in colour.

Fig. 2. A tuber of Mutation No. 2: self-coloured and of pinkish purple tone similar to the original tuber of that mutation.

Fig. 3. A tuber of Mutation 1 A: similar tubers are found in Mutation 2 A and less commonly in Mutation 2. Between the purple patches is found a pinkish purple coloration similar in tone to that shown in Fig. 2.

Fig. 4. A tuber of Mutation 1: similar to the original tuber of that mutation. There is no pigment between the purple patches except for traces in the lenticels.

Fig. 5. A tuber of Mutation 3 A: there is no pigment in the skin except for that shown in a small lateral depression and a very slight trace of the same in the brow of a lateral eye.

Plate VII. Stem Colour.

Fig. 1. The reddish purple pigment is mainly internodal in distribution: it is best, and sometimes only, developed in the lower segments of the stem. The pigment is deposited in small islets separated by green areas. Stem Type No. 1.

Fig. 2. The colour areas are more closely packed and the pigment is in consequence of a deeper tone. The pigment is developed most strongly in the lower parts of the stem but is to be found in a dilute form throughout and it generally extends into the midribs of the leaves. Stem Type No. 2.

Fig. 3. The pigmentation is general throughout the stem system. Its tone is deeper because of the closer approximation of the colour islets. This type is readily distinguished from the preceding. Stem Type No. 3.

Fig. 4. The stem is often almost black, owing to the concentration of the pigment both in the nodes and internodal areas. In plants with this type of stem colour the pigment generally spreads beyond the midribs into the base of the leaflets and the whole plant is darkened. Stem Type No. 4.

Fig. 1.

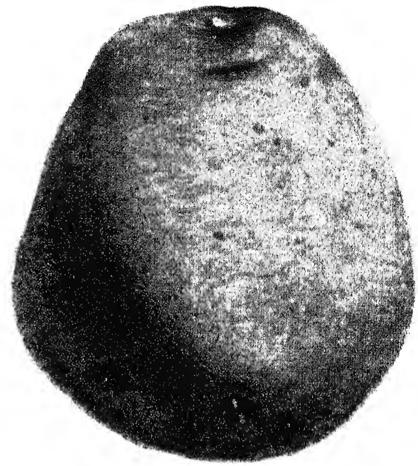

Fig. 2.

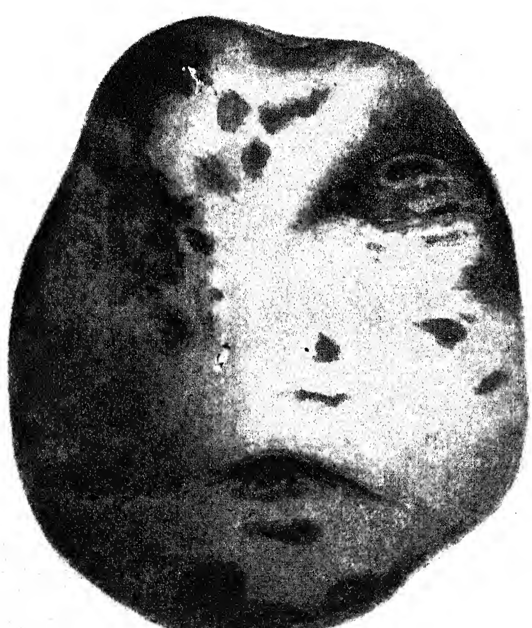

Fig. 3.

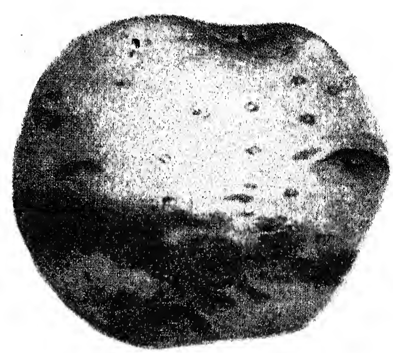

Fig. 4.

Fig. 5.

1 2 3 4

SELF-STERILITY AND CROSS-INCOMPATIBILITY IN PLUMS AND CHERRIES.

By M. B. CRANE,
John Innes Horticultural Institution.

(With Two Text-figures and Six Plates.)

In former papers (1, 13) the results of these experiments up to the year 1922 were published in detail. The work has been continued on trees grown in pots in an orchard-house constructed for the purpose of these investigations. A description of this house, methods of control, and manipulative details have been given in former publications. It may, however, be stated that with the provision of this house many disturbances are entirely eliminated. Greater convenience is afforded in regard to the manipulations, and the results are more reliable. At the beginning of this work flowers were isolated with paper bags in the open, and the effects of frosts, cold winds, heavy rains, etc., frequently blurred the accuracy of the results. Negative results in particular were often of doubtful value.

During the period to which the present report relates, the investigations have mainly been carried out with varieties of plums and cherries. Apples have been dealt with to a lesser extent, but the records of this part of the work are for the present withheld.

CHERRIES.

Cross-incompatibility.

It was shown that certain varieties of the sweet cherry, in addition to being self-sterile, failed to form fruits when pollinated with other distinct varieties. It was also found that, so far, the varieties involved in this inter-sterility could be assigned to groups within which all self and cross-pollinations failed.

The results from repetition and further pollinations between these incompatible varieties have in all cases been confirmatory. Two more such "incompatibles" have been found, they belong to groups previously recognised, and are Black Eagle to Group I, and Guigne de Winkler to Group II. The varieties involved in these groups up to date are:

Group I.	*Group II.*	*Group III.*
Early Rivers	Big. de Schrecken	Emperor Francis
Bedford Prolific	Big. Frogmore	Big. Napoleon
Knight's Early Black	Guigne de Winkler	
Black Tartarian "A"		
Black Tartarian "B"		
Black Eagle		

The total results of the pollinations between these varieties are summarised in the following diagram. The details of the past two years'

♀ \ ♂	*Early Rivers.*	*Bedford Prolific.*	*Knight's Early Black.*	*Black Tartarian "B"*	*Black Tartarian "A"*	*Black Eagle.*	*Big. de Schrecken*	*Big. Frogmore*	*Guigne de Winkler.*	*Emperor Francis.*	*Big. Napoleon.*	
Early Rivers.	977 0	442 0	300 0	481 0	360 0	23 0	209 25	245 34	75 18	38 2	24 1	GROUP I
Bedford Prolific.	392 0	1071 0	265 0	36 0	355 0	38 0	105 49	354 161	91 42	21 4	104 52	GROUP I
Knight's Early Black.	108 1	379 0	957 1	141 0	32 0	30 1	100 27	99 20	112 10		161 46	GROUP I
Black Tartarian "B"	373 0	119 0		240+ 0	40 0			70 6			145 17	GROUP I
Black Tartarian "A"	419 0	65 0	31 0	42 0	815 0		33 4	311 21		206 17		GROUP I
Black Eagle.		42 0	29 0			296 0	29 3	45 9			41 10	GROUP I
Big. de Schrecken.	514 139	394 102	195 59		133 31		2190 0	1854 1	265 0	183 32	131 39	GROUP II
Big. Frogmore.	230 61	129 59	277 86		17 5	27 8	1123 7	1183 0	222 0	362 88	82 13	GROUP II
Guigne de Winkler.	51 9	134 97	10 8		32 17		165 0	164 0	262 0	101 41	36 26	GROUP II
Emperor Francis.	167 67	304 100	33 11	20 11	31 6		164 68	128 54	189 73	1233 6	658 4	GROUP III
Big. Napoleon.	74 41	69 27	92 41		50 32		80 46	38 15	53 14	588 0	334 2	GROUP III

Diagram showing self and cross combinations made between incompatible varieties of cherries. The numbers at the top of the squares are the number of flowers pollinated, those at the bottom are the number of fruits which set and matured.

work are given more precisely in the appended tables, and those of earlier years in Report II.

From 8878 flowers pollinated in Group I 3 fruits have formed. In Group II 8 fruits from 7428 flowers, and in Group III 12 from 2813 flowers. There are reasons for suspecting that some of these fruits are

the result of errors, but some occurred under very stringent conditions. It is, however, obvious that for all practical purposes incompatibility may be regarded as complete within these groups.

The work is less complete in regard to cross-pollinations between varieties belonging to different groups. Several combinations have yet to be attempted, and a number of those already made need repeating on a larger scale. From the majority of such pollinations, so far attempted, good crops have been obtained. There are, however, real indications that such matings are not always completely compatible, as Early Rivers and Black Tartarian "A"—varieties in Group I—have repeatedly failed to set satisfactorily when pollinated by certain varieties in the other groups. Although in reciprocal combinations their own pollen has set fruits freely.

In a previous publication it was pointed out that in all pollinations within the groups the young fruits fall at a very early stage as if unfertilised, but when Early Rivers—Group I—is pollinated by certain varieties not belonging to this group, the fruits reach a comparatively advanced stage before the majority cease growing and fall. In such fruits considerable embryonic development is evident. The incompatibility within the groups is thus quite different, in its outward behaviour, to the partial failure which occurs when Early Rivers is crossed with certain varieties outside its own group. This may be merely the expression of different degrees of the same form of incompatibility, but more probably the inter-group failure is due to a fundamentally distinct cause.

Compatible combinations.

The proportion of flowers which set after compatible pollinations often varies, as is abundantly shown in our records. Results have shown that the kind of crop the tree carried in the previous year, and varietal differences in fruit size—especially in plums—are frequently involved in these variations. I have previously pointed out that a high percentage of fruit is more often expected from a tree bearing a moderate number of flowers, than from one which flowers freely, although the latter may carry a very heavy crop. Many other things have to be considered which could only be recorded at great length. These considerations show that an intimate acquaintance, not only with varieties, but with the individual trees and the many factors involved, are essential to arrive at the real measure of fertility.

Often in the course of these experiments preliminary crosses have

set very few fruits, although the trees have been in good health, whilst repetition has subsequently resulted in heavy crops.

In any attempt to determine the relative value of different cross-pollinations, repetition is a first essential. When, for example, as is later recorded in this report, 54 flowers of Big. Frogmore only gave one fruit when pollinated with Waterloo, it may mean that Waterloo is another incompatible belonging to Group II, but pending further tests the significance of this result is doubtful.

The large majority of the compatible cross-pollinations have resulted in full crops, thereby proving economically efficient. Some, however, have given comparatively poor results, and with regard to these further work must be awaited. Conclusions at the present stage would be premature and of but little value.

Among the sweet cherries varying amounts of bad pollen grains occur. In no variety, however, has the proportion aborted been large enough to detract from its value as a polliniser, nor in the practical work of crossing has such a case been met with. Defective seeds are common in fruits arising from cross-pollinations, occurring more frequently in some combinations than others. The following is an extreme example. From 90 flowers of Big. Noir de Schmidt pollinated with Late Black Bigarreau 47 well-developed fruits reached maturity, but none contained a good seed. Considerable embryonic development had occurred, but in all the testa although large was much shrivelled and practically empty. From subsequent crosses two doubtful seeds have been obtained, but they failed to germinate. Fruits obtained from the reciprocal cross all contained perfect seeds.

Self-sterility.

A few more varieties of the sweet cherry, *P. avium*, have been tested for self-sterility, and like all those formerly tested they proved to be self-sterile. Tests have also been repeated on many varieties previously dealt with, and in all cases they have substantiated former results.

At the beginning of the experiments the number of flowers self-pollinated was not recorded, altogether these would amount to a large number. Subsequently over 18,000 selfed flowers have been recorded in these tests, and from the whole only 21 fruits have been obtained.

The work of others, notably Gardner and Schuster in America (4, 11), Florin in Sweden (3), Sprenger in Holland (12) and Hooper in England (6), also show that it is exceptional within this species to obtain fruits from

self-pollinated flowers. Therefore—at least from a grower's point of view—self-sterility seems to be universal in the sweet cherries.

Pollinations between varieties of P. avium, P. cerasus *and Dukes.*

In our last report I drew attention to the fact that in our experiments varieties of the sweet cherry *P. avium*, when pollinated by the Dukes and varieties of *P. cerasus*, had generally produced and matured fruits freely, whereas from reciprocal pollinations fruits were less freely formed. The percentages of fruit obtained from such crosses were 28·9 and 8·7 respectively. These results, however, were not regarded as implying any general rule. This would need considerable repetition and confirmation from work with many more varieties. Florin (3), however, has recently stated that these results are not of general application, pointing out that in my records some exceptions occur, and that the American and Swedish investigations tend to give reverse results.

Since the above results appeared this part of the work has not been extensively pursued, but the following are records of further pollinations between these groups.

Bigarreaus and Guignes ♀ × *Morellos, Kentish and Dukes* ♂.

Variety	Pollinated by	Flowers	Fruit	% set
Big. Frogmore	Kentish Red "A"	23	11	47·8
" "	Empress Eugenie	37	16	43·2
" Late Black	" "	75	21	28·0
" Napoleon	" "	31	24	77·4
" Noir de Guben	Kentish Red "A"	99	46	46·4
" de Schrecken	" " "	37	5	13·5
Bohemian Black	" " "	75	20	26·6
Elton	Royal Duke	44	15	34·0
Guigne d'Annonay	" "	126	61	48·4
" "	Wye Morello	182	132	72·5
Noble	Kentish Red "A"	54	0	—
	Total	783	351	44·8

Morello and Dukes ♀ × *Bigarreaus and Guignes* ♂.

Empress Eugenie	Bedford Prolific	54	13	24·0
" "	Emperor Francis	45	5	11·1
" "	Noble	52	1	1·9
Royal Duke	Bohemian Black	31	1	3·2
Wye Morello	" "	8	1	12·5
" "	Géante d'Hedelfingen	24	1	4·1
	Total	214	22	10·2

Although one exception has again occurred, the sweet varieties when used as females have again set fruit comparatively freely. Among the

reciprocal pollinations the results are more variable. Collectively they have given a much lower percentage, but owing to the few crosses that were attempted in this way their results cannot be seriously considered.

The crosses between these groups have varied in their ability to form good seeds and in some combinations they have been extremely rare, although fruits have formed with perfect freedom. Others have given a large proportion of good seeds, and from certain of these a number of seedlings have been raised.

Evidence regarding the origin of cherry varieties is scanty and little value would accrue from a lengthy discussion.

The Dukes are generally regarded by systematic pomologists as hybrids between *avium* and *cerasus*, mainly on the evidence of intermediate characters. In addition, the occurrence of a proportion of bad pollen together with defective seeds is sometimes advanced as a sign of their hybridity. This may be correct, and without any attempt to dispute this view, it is interesting to recall that within varieties regarded as *avium*, aborted pollen and defective seeds are common.

Certain varieties raised and reported upon by Thomas Andrew Knight (8) are of particular interest, *e.g.* Knight's Early Black, Black Eagle, and Waterloo. These varieties were raised from crossing a Bigarreau (Yellow Spanish?) with May Duke. Therefore if the Dukes are derived from *avium* and *cerasus*, these varieties have arisen from a back-cross as: *avium* × (*avium* × *cerasus*).

According to Lindley (9) and Hedrick (5) Waterloo has certain intermediate characters. The other two, however, are apparently *avium* to the eye, but genetically they may be different. If these varieties have originated in this way the question arises, to what extent are interspecific crosses involved in the origin of cherry varieties, and one hesitates when considering varieties of the sweet cherry although they appear to be pure *avium*.

Knight's Early Black and Black Eagle are incompatible and belong to Group I, and there are indications that Waterloo may belong to Group II. The origin of these varieties is noteworthy and may be of significance in regard to the existence of cross-incompatibility in cherries.

Our knowledge of the other incompatibles is not sufficient to be helpful in this direction. Bedford Prolific is recorded as a seedling from Black Tartarian—both belong to Group I—but we have several Black Tartarians any one of which may have been the parent. Mention is, however, frequently made in pomological publications of similarities in the characters of these two varieties, and as Black Tartarian "B"

resembles Bedford Prolific in many respects, it is tempting to attribute the origin to that variety.

Confusion of varietal names.

The nomenclature of cherries still presents many difficulties, and a systematic classification of varieties would be of considerable value to the fruitgrower, tree raiser, and research worker alike. The varieties within any incompatible group commonly show much diversity, but some varieties mentioned in this report are very like each other. There are, however, real differences between these, and there is no question of their being distinct. I have endeavoured to ensure that the varieties used in these experiments are correctly named, but the identity of some remains obscure, and it is necessary to refer briefly to the following individuals.

Kentish Red "A." This is not the true Kentish Red. As mentioned in a former paper it is self-fertile, has short fruit stalks, and appears to be greatly confused with the true Kentish Red which has comparatively long stalks and is self-sterile.

Knight's Early Black. This individual more closely agrees with early descriptions of this variety than others received under that name, and is probably correctly named.

Black Tartarian. Regarding the identity of this variety there appears to be no general agreement. Under this name we have received three different individuals; for reference they are designated "A," "B" and "E." Amongst other salient characters "A" has small stellate flowers and long narrow leaves, which show it is not the Black Tartarian of early pomological writers. "B" and "E" both have large and comparatively broad leaves, and large imbricate flowers. The fruits of "B" are very similar to Bedford Prolific—resemblances also occur in other characters—but in several minor respects there are real differences between these varieties. The fruits of "E" are more conical and irregular in shape than those of "B." "A" and "B" are reciprocally incompatible and belong to Group I. "E" has only recently been introduced into the experiments; it has, however, proved to be compatible with some varieties in this group.

PLUMS.

Cross-incompatibility.

The incompatible plums previously reported upon have been further dealt with, and the results have in all cases been confirmatory. In

addition seven more incompatibles have been found. Four of these are well-known varieties, but three are seedlings raised here from Comte d'Althan fertilised by Jefferson. It may be recalled that as far as our work has advanced with cherries incompatibility has always been reciprocal: *e.g.* if *A* fails with *B*, *B* always fails with *A*, and further, every other variety failing with *A* also fails with *B*. The incompatible cherries are also self-sterile, although as a rarity an occasional fruit has formed. The work with incompatible plums also followed this rule up to the time of our last report. In recent work, however, two notable departures from the rule have occurred. (1) Incompatibility occurring in one combination, whilst the reciprocal produces fruit freely. (2) Incompatibles which are partially self-fertile.

The varieties and seedlings involved in this incompatibility, and the groups in which they occur are as follows:

Group I.	*Group II.*	*Group III.*	*Group IV.*
Coe's Golden Drop	Seedling No. 1026	President	Rivers's Early Prolific
Coe's Violet	,, ,, 1030	Late Orange	*Blue Rock*
Crimson Drop		*Cambridge Gage*	
Jefferson			
Allgrove's Superb			
Seedling No. 1024			

It will be seen in the diagram on p. 309 that the three varieties printed in italics above, when used as females, fail on fertilisation with pollen of other sorts in the same respective groups, whereas in reciprocal fertilisations their pollen is effective. In two of these—Cambridge Gage and Blue Rock—both the incompatibility and self-sterility are only imperfect. This is noteworthy and suggests that the properties of self-sterility and cross-incompatibility are independent, although closely associated.

Crimson Drop and Coe's Violet are well known to be bud sports from Golden Drop. More recently Allgrove's Superb has originated as a bud sport from Jefferson, and that it would behave similarly to Jefferson was almost to be expected. In the colour of its fruits it strikingly differs from Jefferson, and Mr J. C. Allgrove, the introducer, has kindly informed me that it also differs in the time of flowering and ripening. The pedicels of the flowers, and other parts of the tree appear to be a little less hairy than those of Jefferson, but in other respects they are similar.

Self-sterility.

Self-sterility tests have been repeated with several varieties, and they have continued to give consistent results. In general plums can be

classified as follows: (I) Completely self-fertile. (II) Partially self-fertile. (III) Self-sterile. Among the varieties in class II, some set a larger proportion of fruit with their own pollen than others.

Among varieties classified as self-fertile in former reports, some have appeared to set better crops when cross-pollinated. In regard to varieties

♀ \ ♂	Coe's Golden Drop.	Coe's Violet.	Crimson Drop.	Jefferson.	Allgrove's Superb.	Comte d'Althan × Jefferson 1024	Comte d'Althan × Jefferson 1026	Comte d'Althan × Jefferson 1030	President	Late Orange	Cambridge Gage	Rivers Early Prolific.	Blue Rock.	
Coe's Golden Drop.	1072+ / 0	200+ / 0	366 / 0	1035 / 10	42 / 1	46 / 10		10 / 3	54 / 25	90 / 37	57 / 38	MANY / MANY		GROUP I
Coe's Violet	73+ / 0	735 / 0	141+ / 1	585+ / 1					44 / 31	195 / 88	71 / 49	157 / MANY		GROUP I
Crimson Drop.	87 / 0	88+ / 0	470 / 1	209 / 0										GROUP I
Jefferson	768 / 1	414 / 2	515 / 1	260+ / 0	34 / 0	25 / 15	29 / 23	13 / 10		16 / 15		MANY / MANY		GROUP I
Allgrove's Superb.		21 / 0		45 / 0	105 / 0					42 / 28	14 / 11			GROUP I
Comte d'Althan × Jefferson 1024	34 / 0			14 / 0		154 / 0		8 / 5					18 / 9	GROUP II
Comte d'Althan × Jefferson 1026	9 / 8			11 / 7		13 / 12	131 / 0						12 / 11	GROUP II
Comte d'Althan × Jefferson 1030				11 / 1			31 / 0	36 / 0	12 / 3					GROUP II
President	58 / 42	74 / 38		75 / 28					158 / 0	184 / 0	52 / 14	18 / 11		GROUP III
Late Orange	97 / 36	94 / 32		78 / 19	30 / 6				397 / 0	489 / 0	127 / 26			GROUP III
Cambridge Gage		203 / 109							138 / 7	242 / 9	1198 / 32	15 / 10		GROUP III
Rivers Early Prolific.		226 / 86		57 / 23					48 / 13	102 / 38	126 / 57	3152 / 113	249 / 115	GROUP IV
Blue Rock		126 / 96								103 / 66	63 / 41	232 / 10	612 / 11	GROUP IV

Diagram showing self and cross-pollinations between incompatible varieties of plums. The numbers at the top of the squares are the number of flowers pollinated, those at the bottom are the number of fruits which reached maturity. (+) means that, in addition to the number recorded, many more flowers were pollinated.

in Class II this is of course correct, and with further experience some changes have been made in the original classification. When the fully self-fertiles set more when cross-fertilised the cause is probably that a branch is invariably selected for emasculation and crossing which lends itself to isolation. Such branches often have advantages, and are able to carry a higher proportion of fruit than branches in more crowded parts of the tree. For example, in the appended records Guthrie's Late

appears as having set 27·7 per cent. when selfed, and 29·7 per cent. when crossed with Coe's Golden Drop. If, however, we take each branch separately the results are:

	Flowers	Fruit	% set
Crossed. Coe's Golden Drop	94	28	29·7
Selfed	84	27	32·1
"	48	8	16·6
"	41	13	31·7
"	118	31	26·2
"	170	66	38·8
"	45	12	26·6
"	94	23	24·4
"	114	21	18·4
"	4	0	—
"	6	1	16·6
"	14	2	14·2
"	102	29	28·4

Some of the individual selfed branches have thus set even a higher proportion of fruit than the crossed branch. This shows that when the records are abbreviated the slightly higher result in favour of the crossed branch is not significant.

Genetical Aspects.

It has been shown in previous papers that in self-sterile plums the plant's own pollen germinates on the stigmatic surface, but subsequently the tubes become arrested in the nutrient stylar tissue and fail to reach the ovary. This phenomenon has been seen by previous observers in other self-sterile plants. It also occurs in cross-pollinations made between the incompatible plums. In plums and cherries, genetic enquiries relating to self-sterility and cross-incompatibility progress slowly, and an adequate interpretation of our results cannot be attempted at the present stage. Nevertheless, the work has suggested certain features of genetical interest.

So far there is nothing in our results which negatives the view that the property of self-sterility may be a Mendelian recessive, but it seems probable that more than one genetic factor is involved. Pollination tests have been carried out on a number of seedlings in the open and in the orchard-house. It was found, however, that the results from work in the open could not be accepted with confidence, and the following is a brief summary of the results obtained from trees grown in pots under the more stringent conditions afforded by the orchard-house.

Parentage	No. of seedlings tested	Results
Self-fertiles – Selfed ...	37	Varying degrees of self-fertility occur. Some are completely self-fertile, but some set comparatively few fruits when selfed. Three have so far wholly failed to set fruit with their own pollen.
Self-sterile × Self-fertile	3	1 self-fertile, 1 partially self-fertile, 1 self-sterile.
Self-sterile × Self-sterile	5	All self-sterile. On one occasion 1 set about 1 % of fruit, but this may be the result of some accident, as when repeated it wholly failed.

In recent work Morgan (10) has succeeded in bringing about self-fertilisation in *Ciona intestinalis*, by simply freeing the eggs from their membranes. Thereby showing that in this animal the block to self-fertility is caused by the surrounding membranes or by their secretions, and that there is no incompatibility between the egg itself and its own sperm.

In self-sterile plums we have attempted to induce the pollen tubes to travel the full length of the styles to see if self-fertilisation would then occur, but up to the present this has not been successful. In these experiments nutrient solutions were used in various ways, and the cross-grafting of styles was attempted. It is, however, evident that in plums and cherries the incompatible cross-pollinations cannot be regarded as ordinary sexual crosses, as on the female side we are not dealing with a sexual, but with a somatic phenomenon. In the styles where the pollen tubes become arrested we have somatic tissue, consequently on this side we are not concerned with the possibility of gametic segregation. In the pollen, however, we have gametic tissue, and presumably plants heterozygous for incompatibility would produce grains of different kinds, some carrying the incompatibility, some having lost it.

During the course of these experiments numerous crosses have been made between self-sterile and self-fertile plums, and it is noteworthy that all the varieties involved in cross-incompatibility—both cherries and plums—are self-sterile or nearly so. This is also in agreement with Gardner's (4) and Schuster's (11) work with cherries. Nevertheless, although self-sterility and cross-incompatibility appear to be closely associated, our results suggest that they are determined independently.

In plums we have four groups of incompatibles, but as was previously shown, in three of these groups varieties occur which fail only when they are used as females. This suggests that these varieties are heterozygous for incompatibility, and that the others, which form a completely inter-sterile group, are homozygous for this character. If we regard F as the factor conferring self-fertility and assign a different factor to each

kind of incompatibility, as A to Group I, B to Group II, etc., we can attempt a genetical analysis of our results. The groups and varieties involved would then be represented as:

Group I.		*Group III.*	
Coe's Golden Drop ...	AA	President	CC
Coe's Violet	AA	Late Orange ...	CC
Crimson Drop ...	AA	Cambridge Gage ...	Cc
Jefferson	AA		
Allgrove's Superb ...	AA		
Seedling 1024 ...	Aa		
Group II.		*Group IV.*	
Seedling 1026 ...	BB	Rivers's Early Prolific	DD
„ 1030 ...	BB	Blue Rock	Dd

All these, being self-sterile, must be represented as ff.

Assuming that A in the styles inhibits A pollen the first five varieties in Group I would form an inter-sterile group, and seedling 1024 would fail on its female side because it is somatically $ffAa$. Its pollen, however, segregates into A and a, and the pollen-grains having the constitution a, inasmuch as they do not carry A, are not excluded by the styles of the other varieties in Group I though they possess the factor A. The same would apply to Cambridge Gage Cc in Group III, and to Blue Rock Dd in Group IV. As shown in Table II this interpretation agrees with the results.

If a pollen can fertilise AA the first question which arises is: why is 1024 Aa unable to fertilise itself? This can only be due to self-sterility being determined by factors other than those concerned in cross-incompatibility; and I am inclined to regard this as showing that cross-incompatibility is due to additional factors. It is not improbable that self-fertile varieties may carry factors for cross-incompatibility, and that in pollination tests these factors are rendered impotent by the factors which determine self-fertility. In this way homozygous incompatibles might arise from self-fertile varieties, *e.g.* as segregates from combinations as $FfAa$ and $FfAA$. This scheme would also account for the fact that self-steriles are always compatible with self-fertiles so far as we at present know, and for the apparent association of cross-incompatibility with self-sterility.

In regard to the fruits which have formed as a rarity in incompatible combinations, *e.g.* when the Coe's have been crossed with Jefferson, it seems possible that this may be due to somatic segregation occasionally occurring.

Seedling 1024 was raised from Comte d'Althan, which is of course outside Group I, fertilised by Jefferson; and that heterozygous *Aa* forms should occur in this family is not against expectation.

Possibly more than one factor for incompatibility is involved in each group, and the scheme detailed may subsequently require further elaboration. The main purpose of this discussion, however, has been to bring forward a possible explanation of varieties being incompatible one way of a cross, and compatible in the reciprocal. Further complications cannot be seriously considered until tests have been carried out on an adequate number of seedlings, and a knowledge of the genetic interaction of the factors determining the different incompatible groups is available.

In our work with cherries cross-incompatibility has so far always been reciprocal. Gardner (4) has, however, reported an example which is compatible one way and fails in the other. It therefore appears probable that their incompatibility may be similar to that in plums. The partial failure, and the formation of fruits without good seeds, in certain cherry crosses is probably due to degrees of genetic incompatibility, which arrests the embryonic growth at varying stages.

In a number of self-sterile plants self-sterility is attributable to slow pollen tube growth, *e.g.* East (2) in *Nicotiana* and Knight (7) in Apples. In self-sterile plums and cherries, however, there is probably a definite block to self-fertilisation analogous to Morgan's example in *Ciona*. Cross-incompatibility in *Prunus* also differs from that in *Nicotiana* in important respects, since in his extensive investigations East has shown that cross-incompatibility is always reciprocal and that selective fertilisation does not occur. In plums, however, there are exceptions to this rule.

Histological investigations carried out in conjunction with Mr E. J. Collins show that cross-incompatibility in the plum is a very definite phenomenon, and that it cannot be entirely attributed to slow pollen-tube growth. Under the orchard-house conditions the styles remain in an active state for a considerable period as the following experiment shows. A large number of flowers were pollinated on 16 consecutive days, beginning with flowers which had been open one day and continuing up to flowers which had been open 16 days. The maximum set occurred on flowers pollinated on the 6th day, but absolute failure to set and mature fruits did not occur until the 14th day.

Styles which were pollinated with an incompatible variety have been prepared and microscopically examined at frequent intervals from 24 hours up to 12 days after pollination. For convenience in the manipulations these styles have always been cut approximately in halves previous

to fixation, and in the subsequent examinations pollen tubes have never been observed in the lower half. This shows that the incompatibility is due to inhibition occurring shortly after the penetration of the pollen tubes, and not to slow growth.

CLASSIFICATION OF CHERRIES AND PLUMS IN RESPECT OF SELF-STERILITY.

CHERRIES.

Self-sterile	*Partially self-fertile*	*Self-fertile*
Amber Heart (Kentish Big.)	Arch Duke	Flemish Red
Bedford Prolific	May Duke	Kentish Red "A"
Belle d'Orleans	Royal Duke	Late Duke
,, de St Trone	Empress Eugenie	Morello
Bigarreau Frogmore		Wye Morello
,, Jaboulay		
,, Late Black		
,, Noir de Guben		
,, ,, de Schmidt		
,, Napoleon		
Black Eagle		
,, Heart		
,, Tartarian "A"		
,, ,, "B"		
,, ,, "E"		
Bohemian Black		
Early Rivers		
Elton		
Emperor Francis		
Florence		
Géante d'Hedelfingen		
Governor Wood		
Guigne d'Annonay		
,, de Winkler		
Knight's Early Black		
Monstreuse de Mezel		
Noble		
Turkey Heart		
Waterloo		
White Heart		
Kentish Red		
Toussaint (?)		

All the self-steriles, of whatever origin, except the two last-named, are *sweet* cherries. The five self-fertiles are *sour* cherries.

PLUMS.

Self-sterile	*Partially self-fertile*	*Self-fertile*
Allgrove's Superb	Belgian Purple	Belle de Louvain
Bryanstone Gage	Blue Rock	Czar
Coe's Golden Drop	Cambridge Gage	Denniston Superb
,, Violet	Cox's Emperor	Early Transparent
Comte d'Althan	Early Favourite	,, Mirabelle
Crimson Drop	,, Orleans	Gisborne's
Early Green Gage	Rivers's Early Prolific	Golden Transparent
Jefferson	Prince Engelbert	Goliath
Kirke's Blue	Reine Claude Violet	Guthrie's Late

Self-sterile	*Partially self-fertile*	*Self-fertile*
Late Orange	Frogmore Damson	Monarch
,, Orleans (Frogmore Orleans)		Myrobalan Red
McLaughlin's Gage		Oullin's Golden Gage
Old Green Gage		Pershore
Pond's Seedling		Prince of Wales
President		Prune Géante
Prune d'Agen		Reine Claude Bavay
Transparent Gage		Victoria
Wyedale		White Magnum Bonum
Yellow Magnum Bonum		Farleigh Damson
		King of the Damsons

TABULATED POLLINATIONS OF CHERRIES AND PLUMS, 1923–1924.

CHERRIES.

SWEET VARIETIES

	Selfed				Crossed		
	Flowers	Fruit	% set	Pollinated by	Flowers	Fruit	% set
BEDFORD PROLIFIC	44	0	—	Big. de Schrecken ...	74	33	44·5
,, ,,	260	0	—	,, Frogmore ...	203	68	33·4
,, ,,	381	0	—	,, ,, ...	121	64	52·8
,, ,,	156	0	—	Belle de St Tronc ...	163	65	39·8
				Black Tartarian "A"	50	0	—
				,, ,, ,,	127	0	—
				,, ,, ,,	144	0	—
				,, ,, "E"	24	10	41·6
				,, ,, "B"	23	0	—
				Early Rivers ...	101	0	—
				,, ,, ...	130	0	—
				,, ,, ...	121	0	—
				Black Eagle... ...	38	0	—
				Knight's Early Black	157	0	—
				,, ,, ,,	23	0	—
				Noble	36	23	63·8
				Governor Wood ...	46	30	65·2
				Emperor Francis ...	21	4	19·0
				Big. Napoleon ...	104	52	50·0
				Elton	26	21	80·7
				Guigne de Winkler...	71	36	50·7
				,, ,, ,, ...	20	6	30·0
				Late Black Big. ...	118	58	49·1
				Turkey Heart ...	19	12	63·1
				,, ,, ...	112	81	72·3
				Early Purple Gean...	22	7	31·8
BELLE D'ORLEANS ...	239	0	—	Early Rivers ...	67	13	19·4
				Black Tartarian "A"	46	18	39·1
BIG. DE SCHRECKEN	195	0	—	Guigne de Winkler...	106	0	—
,, ,, ,,	775	0	—	,, ,, ,, ...	80	0	—
,, ,, ,,	314	0	—	,, ,, ,, ...	79	0	—
,, ,,	542	0	—	Big. Frogmore ...	206	0	—
				,, ,, ...	206	0	—
				,, ,, ...	131	0	—
				,, ,, ...	124	0	—
				Black Tartarian "A"	133	31	23·3
				Bedford Prolific ...	51	19	37·2
				,, ,, ...	276	76	23·9
				Early Rivers ...	72	44	61·1
				,, ,, ...	267	38	14·2
				Kentish Red "A" ...	37	5	13·5

	Selfed				Crossed		
	Flowers	Fruit	% set	Pollinated by	Flowers	Fruit	% set
				Emperor Francis ...	135	24	17·7
				,, ,, ...	48	8	16·6
				Géante d'Hedelfingen	146	31	21·2
				Belle de St Tronc ...	75	27	36·0
				,, ,, ,, ,, ...	82	25	30·4
				Noble	43	15	34·8
				Elton	100	26	26·0
				Governor Wood ...	47	8	17·0
				Big. Napoleon ...	131	39	29·7
				Turkey Heart ...	220	44	20·0
				Jaboulay	97	30	30·9
BELLE DE ST TRONC	80	0	—	Bedford Prolific ...	28	8	28·5
,, ,, ,, ,,	125	0	—	Big. Napoleon ...	35	6	17·1
				,, Frogmore ...	12	2	16·6
				Bohemian Black ...	25	3	12·0
				Big. Noir de Guben	108	32	29·6
				Knight's Early Black	28	13	46·4
				Jaboulay	89	29	32·5
BIG. FROGMORE ...	74	0	—	Big. de Schrecken ...	153	0	—
,, ,, ...	38	0	—	,, ,, ,, ...	60	0	—
,, ,, ...	374	0	—	,, ,, ,, ...	179	0	—
,, ,, ...	147	0	—	,, ,, ,, ...	151	1	0·6
				Guigne de Winkler...	35	0	—
				,, ,, ,, ...	187	0	—
				Black Tartarian "A"	17	5	29·4
				,, ,, "E"	30	11	36·6
				Bedford Prolific ...	59	40	67·7
				Black Eagle... ...	27	8	29·6
				Emperor Francis ...	129	40	31·0
				,, ,, ...	233	48	20·6
				Empress Eugenie ...	37	16	43·2
				Early Rivers ...	40	18	45·0
				,, ,, ...	85	25	29·4
				Elton	18	6	33·3
				Early Purple Gean...	12	9	75·0
				Knight's Early Black	117	27	23·0
				,, ,, ,,	160	59	36·8
				Governor Wood ...	354	122	34·4
				Kentish Red "A" ...	23	11	47·8
				Géante d'Hedelfingen	74	15	20·2
				Late Black Big. ...	187	66	35·2
				Turkey Heart ...	73	28	38·3
				,, ,, ...	71	45	63·3
				Noir de Schmidt ...	116	29	25·0
				Napoleon	82	13	15·8
				Waterloo	54	1	1·8
BIG. JABOULAY ...	183	0	—	Big. Noir de Guben	138	34	24·6
				Bohemian Black ...	36	4	11·1
				Belle de St Tronc ...	57	6	10·5
BIG. NAPOLEON ...	42	1	2·3	Emperor Francis ...	155	0	—
,, ,, ...	184	0	—	,, ,, ...	337	0	—
,, ,, ...	5	0	—	,, ,, ...	29	0	—
,, ,, ...	38	0	—	,, ,, ...	34	0	—
				Bedford Prolific ...	69	27	39·1
				Black Tartarian "A"	50	32	64·0
				Belle de St Tronc ...	50	2	4·0
				Big. de Schrecken ...	80	46	57·5
				,, Frogmore ...	38	15	39·4
				Early Rivers ...	74	41	55·4
				Elton	20	4	20·0

	Selfed				Crossed		
	Flowers	Fruit	% set	Pollinated by	Flowers	Fruit	% set
				Bohemian Black ...	6	3	50·0
				Knight's Early Black	38	24	63·1
				„ „ „	54	17	31·4
				Guigne de Winkler ...	34	8	23·5
				„ „ „ ...	19	6	31·5
				Empress Eugenie ...	31	24	77·4
				Late Black Big. ...	109	51	46·7
				Governor Wood ...	14	2	14·2
				Jaboulay	18	10	55·5
BIG. NOIR DE GUBEN	623	1	0·16	Bohemian Black ...	288	108	37·5
				Jaboulay	78	33	42·3
				Belle de St Tronc ...	161	74	45·9
				Kentish Red "A" ...	99	46	46·4
BIG. NOIR DE SCHMIDT	5	0	—	Big. Late Black ...	48	3	6·2
„ „ „ „	265	0	—	„ „ „ ...	87	15	17·2
				„ Frogmore ...	28	8	28·5
				Bedford Prolific ...	6	0	—
				Early Rivers ...	36	5	13·8
				Governor Wood ...	31	7	22·5
				Emperor Francis ...	70	10	14·2
				Noble	91	14	15·3
				Waterloo	19	3	15·7
BLACK EAGLE ...	83	0	—	Bedford Prolific ...	42	0	—
„ „ ...	13	0	—	Knight's Early Black	29	0	—
				Big. de Schrecken ...	29	3	10·3
				„ Napoleon ...	41	10	24·3
				„ Frogmore ...	45	9	20·0
BLACK TARTARIAN "A"	146	0	—	Bedford Prolific ...	45	0	—
„ „ „	459	0	—	Big. Frogmore ...	34	0	—
				„ „ ...	264	19	7·1
				Early Rivers ...	55	0	—
				„ „ ...	256	0	—
				Knight's Early Black	31	0	—
				Black Tartarian "E"	16	1	6·2
				Belle d'Orleans ...	76	7	9·2
				Emperor Francis ...	206	17	8·2
				Late Black Big. ...	35	8	22·8
				Governor Wood ...	212	29	13·6
BLACK TARTARIAN "E"	73	0	—	Big. Napoleon ...	6	0	—
				„ „ ...	23	0	—
				„ Frogmore ...	17	1	5·8
				Bedford Prolific ...	25	0	—
				Governor Wood ...	43	5	11·6
BLACK TARTARIAN "B"	150	0	—	Bedford Prolific ...	44	0	—
				Black Tartarian "E"	45	5	11·1
				Big. Napoleon ...	65	4	6·1
				„ Frogmore ...	70	6	8·5
BOHEMIAN BLACK ...	31	0	—	Géante d'Hedelfingen	33	0	—
„ „ ...	95	1	1·0	„ „	37	29	78·3
„ „ ...	292	1	0·3	Late Black Big. ...	72	40	55·5
				Emperor Francis ...	32	17	53·1
				Early Rivers ...	102	57	55·8
				Kentish Red "A" ...	75	20	26·6
				Big. Noir de Guben	64	20	31·2
EARLY PURPLE GEAN	—	—	—	Governor Wood ...	2	0	—
				Big. Frogmore ...	4	1	25·0
EARLY RIVERS ...	170	0	—	Bedford Prolific ...	81	0	—
„ „ ...	490	0	—	„ „ ...	266	0	—
„ „ ...	7	0	—	Knight's Early Black	60	0	—

	Selfed Flowers	Selfed Fruit	Selfed % set	Pollinated by	Crossed Flowers	Crossed Fruit	Crossed % set
EARLY RIVERS ...	50	0	—	Knight's Early Black	58	0	—
„ „ ...	26	0	—	„ „ „	82	0	—
				Black Tartarian "A"	24	0	—
				„ „ „	158	0	—
				„ „ "E"	15	0	—
				„ Eagle... ...	23	0	—
				Big. Frogmore ...	118	16	13·5
				„ „ ...	80	16	20·0
				Governor Wood ...	98	30	30·6
				„ „ ...	13	1	7·6
				„ „ ...	60	19	31·6
				Belle de St Tronc ...	36	4	11·1
				Big. Napoleon ...	24	1	4·1
				Emperor Francis ...	38	2	5·2
				Big. de Schrecken ...	115	12	10·4
				„ Noir de Schmidt	97	43	44·3
				Guigne de Winkler...	75	18	24·0
				Early Purple Gean...	43	20	46·5
				Waterloo	25	14	56·0
				Late Black Big. ...	82	29	35·3
ELTON	139	0	—	Guigne d'Annonay ...	87	29	33·3
„	212	0	—	Royal Duke... ...	44	15	34·0
				Emperor Francis ...	68	28	41·1
				Big. Napoleon ...	178	87	48·8
				Turkey Heart ...	87	32	36·7
				Big. de Schrecken ...	200	82	41·0
				Knight's Early Black	46	13	28·2
EMPEROR FRANCIS ...	270	0	—	Big. Napoleon ...	155	0	—
„ „ ...	488	1	0·2	„ „ ...	277	1	0·3
„ „ ...	149	4	2·6	„ „ ...	179	3	1·6
„ „ ...	66	1	1·5	„ „ ...	47	0	—
				„ de Schrecken ...	57	30	52·6
				„ „ „ ...	60	17	28·3
				Bedford Prolific ...	35	13	37·1
				„ „ ...	170	57	33·5
				Belle de St Tronc ...	32	8	25·0
				„ „ „ „ ...	30	6	20·0
				Black Tartarian "A"	31	6	19·3
				Early Rivers ...	85	38	44·7
				„ „ ...	82	29	35·3
				Elton	142	36	25·3
				Governor Wood ...	173	43	24·8
				Knight's Early Black	33	11	33·3
				Late Black Big. ...	138	46	33·3
				Guigne de Winkler...	42	17	40·4
				„ „ „ ...	147	56	38·0
				Jaboulay	50	16	32·0
FLORENCE	105	0	—	Kentish Bigarreau ...	66	26	39·3
GÉANTE D'HEDELFINGEN	36	0	—	Noble	89	0	—
„ „	152	0	—	Early Rivers ...	43	1	2·2
				Big. Frogmore ...	104	1	0·9
				„ Napoleon ...	148	10	6·7
				Bohemian Black ...	18	12	66·6
				Florence	27	9	33·3
GOVERNOR WOOD ...	350	2	0·5	Noble	103	43	41·7
„ „ ...	503	1	0·1	„	256	141	55·0
				Guigne de Winkler...	99	26	26·2
				„ „ „ ...	70	23	32·8
				Black Tartarian "A"	24	4	16·6

	Selfed				Crossed		
	Flowers	Fruit	% set	Pollinated by	Flowers	Fruit	% set
				Black Tartarian "A"	35	16	45·7
				,, ,, "E"	24	6	25·0
				Bohemian Black ...	120	29	24·1
				Black Eagle... ...	115	18	15·6
				Turkey Heart ...	123	66	53·6
				Big. Frogmore ...	111	52	46·8
				,, de Schrecken ...	51	16	31·3
				Géante d'Hedelfingen	168	48	28·5
				Emperor Francis ...	81	32	39·5
GUIGNE D'ANNONAY	368	0	—	Emperor Francis ...	256	130	50·7
				Royal Duke... ...	126	61	48·4
				Wye Morello ...	182	132	72·5
GUIGNE DE WINKLER	114	0	—	Big. Frogmore ...	61	0	—
,, ,, ,,	115	0	—	,, ,, ...	73	0	—
,, ,, ,,	33	0	—	,, ,, ...	30	0	—
				,, de Schrecken ...	88	0	—
				,, ,, ,, ...	77	0	—
				Belle de St Tronc ...	23	1	4·3
				Bedford Prolific ...	60	44	73·3
				,, ,, ...	74	53	71·6
				Black Tartarian "A"	32	17	53·1
				Emperor Francis ...	15	4	26·6
				,, ,, ...	69	23	33·3
				,, ,, ...	17	14	82·3
				Early Rivers ...	31	9	17·6
				Jaboulay	47	30	63·8
				Governor Wood ...	49	23	46·9
				Knight's Early Black	10	8	80·0
				Big. Napoleon ...	36	26	72·2
KNIGHT'S EARLY BLACK	139	0	—	Bedford Prolific ...	53	0	—
,, ,, ,,	89	0	—	,, ,, ...	44	0	—
,, ,, ,,	116	0	—	Bohemian Black ...	31	0	—
,, ,, ,,	40	0	—	Black Eagle... ...	30	1	3·3
				Big. Napoleon ...	51	20	39·2
				,, Frogmore ...	65	14	21·5
				Jaboulay	22	6	27·2
				Black Tartarian "E"	44	12	27·2
				Guigne de Winkler...	112	10	8·9
				Governor Wood ...	99	19	19·1
				Early Rivers ...	108	1	0·9
LATE BLACK BIGARREAU	36	1	2·7	Bedford Prolific ...	79	29	36·7
,, ,, ,,	262	0	—	Big. Noir de Schmidt	41	11	36·8
				,, ,, ,, ,,	89	21	23·5
				Belle de St Tronc ...	18	5	27·7
				Emperor Francis ...	127	31	24·4
				Governor Wood ...	193	61	31·6
				Empress Eugenie ...	75	21	28·0
				Waterloo	21	5	23·8
MONSTREUSE DE MEZEL	66	0	—	Emperor Francis ...	25	4	16·0
				Elton	31	2	6·4
				Bohemian Black ...	13	1	7·6
NOBLE	81	0	—	Kentish Red "A" ...	54	0	—
,, ...	369	1	0·2	Bedford Prolific ...	131	34	25·9
,, ...	105	0	—	,, ,, ...	19	7	36·8
				Early Rivers ...	51	20	39·2
				Big. Frogmore ...	65	27	41·5
				,, ,, ...	24	24	100·0
				,, ,, ...	22	7	31·8
				Governor Wood ...	61	10	16·4

	Selfed Flowers	Fruit	% set	Crossed: Pollinated by	Flowers	Fruit	% set
				Guigne de Winkler ...	30	7	23·3
				Géante d'Hedelfingen	96	18	18·7
				Big. Napoleon ...	53	13	24·5
				Emperor Francis ...	93	14	15·0
				Turkey Heart ...	19	12	63·1
				Black Tartarian "B"	25	5	20·0
Turkey Heart ...	116	1	0·8	Big. Frogmore ...	68	21	30·8
,, ,, ...	96	0	—	,, Napoleon ...	44	4	9·0
				,, de Schrecken ...	68	1	1·4
				Bedford Prolific ...	106	17	16·0
SOUR VARIETIES							
Empress Eugenie ...	162	20	12·3	Bedford Prolific ...	54	13	24·0
				Emperor Francis ...	45	5	11·1
				Noble	52	1	1·9
Royal Duke ...	620	3	0·4	Bohemian Black ...	31	1	3·2
Wye Morello ...				,, ,, ...	8	1	12·5
				Géante d'Hedelfingen	24	1	4·1
Kentish Red "A"	357	53	14·8				
,, ,, ,,	456	123	26·9				
Morello	507	86	16·9				

Plums.

	Selfed Flowers	Fruit	% set	Crossed: Pollinated by	Flowers	Fruit	% set
Allgrove's Superb	105	0	—	Jefferson	45	0	—
				Coe's Violet	21	0	—
				Late Orange ...	42	28	66·6
				Prince of Wales ...	32	25	78·1
				Cambridge Gage ...	14	11	78·5
Blue Rock	256	8	3·1	Rivers's Early Prolific	78	7	8·9
,, ,, ...	356	3	0·8	,, ,, ,,	154	3	1·9
				Late Orange ...	103	66	64·0
				Cambridge Gage ...	63	41	65·0
				Coe's Violet ...	126	96	76·1
				Prince of Wales ...	64	51	79·6
Cambridge Gage ...	703	21	2·9	Coe's Violet	203	109	53·6
,, ,, ...	87	2	2·3	Late Orange ...	242	9	3·7
,, ,, ...	308	9	2·9	Early Favourite ...	152	112	73·6
				President	138	7	5·0
Coe's Golden Drop	167	0	—	Jefferson	76	0	—
,, ,, ,,	63	0	—	,, ...	102	1	0·9
				Allgrove's Superb ...	42	1	2·3
				Cambridge Gage ...	57	38	66·6
				Late Orange ...	66	22	33·3
				President	54	25	46·3
				Prince of Wales ...	30	14	46·6
				White Damson ...	70	54	77·1
				Yellow Magnum Bonum	133	39	29·3
				Seedling 1024 ...	46	10	21·7
				,, 1030 ...	10	3	30·0
Coe's Violet ...	66	0	—	Coe's Golden Drop ...	73	0	—
				Jefferson	87	1	1·1
				Cambridge Gage ...	71	49	67·6
				Kirke's Blue ...	74	39	52·7
				Late Orange ...	104	53	50·9
				President	5	3	60·0
				Seedling 1025 ...	26	16	61·5
				,, 1027 ...	14	8	57·1

	Selfed Flowers	Selfed Fruit	Selfed % set	Pollinated by	Crossed Flowers	Crossed Fruit	Crossed % set
GUTHRIE'S LATE ...	840	233	27·7	Coe's Golden Drop ...	94	28	29·7
JEFFERSON	—	—	—	Allgrove's Superb ...	34	0	—
				Coe's Golden Drop ...	32	1	3·1
				Late Orange ...	16	15	93·7
				Seedling 1024 ...	25	15	60·0
				„ 1026 ...	29	23	79·3
				„ 1030 ...	13	10	76·9
KIRKE'S BLUE ...	669	0	—	Allgrove's Superb ...	45	26	57·7
				Cambridge Gage ...	201	88	43·7
				Late Orange ...	167	66	39·5
				President	124	20	16·1
LATE ORANGE ...	305	0	—	Allgrove's Superb ...	30	6	20·0
				Cambridge Gage ...	127	26	20·4
				Coe's Golden Drop ...	97	36	37·1
				Kirke's Blue ...	22	6	27·2
				President	20	0	—
				„	211	0	—
				Yellow Magnum Bonum	44	0	—
PRESIDENT	52	0	—	Late Orange ...	30	0	—
„ ...	52	0	—	„ „ ...	110	0	—
				Cambridge Gage ...	52	14	26·9
				Coe's Golden Drop ...	58	42	72·4
				„ Violet	74	38	51·3
				Jefferson	75	28	37·3
				White Magnum Bonum	54	36	66·6
				Seedling 1025 ...	21	12	57·1
				„ 1027 ...	22	8	36·3
PRINCE OF WALES ...	321	115	35·8	Coe's Violet	33	11	33·3
RIVERS' EARLY PROLIFIC	503	25	4·9	Blue Rock	147	63	42·8
„ „ „	714	27	3·7	„ „	102	52	50·9
				Cambridge Gage ...	126	57	45·2
				Coe's Violet	226	86	38·0
				Jefferson	57	23	40·3
				Prince of Wales ...	126	40	31·7
				White Magnum Bonum	45	21	46·6
WHITE DAMSON ...	—	—	—	Coe's Golden Drop ...	9	5	55·5
WHITE MAGNUM BONUM	147	76	51·7	President	45	30	66·6
YELLOW MAGNUM BONUM	375	1	0·2	Coe's Golden Drop ...	121	91	75·2
				Blue Rock	89	56	62·9
				President	48	30	62·5
SEEDLING NO. 1024	145	0	—	Blue Rock	18	9	50·0
(Comte d'Althan ×	9	0	—	Coe's Golden Drop ...	10	0	—
Jefferson)				„ „ „ ...	24	0	—
				Seedling 1027 ...	11	8	72·7
				„ 1027 ...	12	5	35·7
				„ 1030 ...	8	5	62·5
				Jefferson	14	0	—
SEEDLING NO. 1025	25	1	4·0	Coe's Golden Drop ...	9	5	55·5
(Comte d'Althan ×	21	0	—	Late Orange ...	11	5	45·5
Jefferson)				Jefferson	12	4	33·3
				President	6	5	83·3
				Seedling 1024 ...	20	10	50·0
				„ 1026 ...	13	5	38·4
				„ 1026 ...	13	8	61·5
SEEDLING NO. 1026	131	0	—	Coe's Golden Drop ...	9	8	88·8
(Comte d'Althan ×				Blue Rock	12	11	91·6
Jefferson)				Jefferson	11	7	63·6

	Selfed				Crossed		
	Flowers	Fruit	% set	Pollinated by	Flowers	Fruit	% set
				Seedling 1024 ...	13	12	92·3
				„ 1025 ...	7	7	100·0
SEEDLING No. 1027	241	4	1·6	Jefferson	30	9	30·0
(Comte d'Althan ×	21	0	—	President	12	1	8·3
Jefferson)				Rivers's Early Prolific	37	13	35·1
				Seedling 1024 ...	17	4	23·5
				„ 1024 ...	14	4	28·5
				„ 1026 ...	19	5	26·3
SEEDLING No. 1030	36	0	—	Jefferson	11	1	9·0
(Comte d'Althan ×				President	12	3	25·0
Jefferson)				White Magnum Bonum	19	7	36·8
				Seedling 1026 ...	10	0	—
				„ 1026 ...	21	0	—

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Fig. 1. Early Rivers (Group I). (At top of tree) 490 flowers self-pollinated, no fruit set. 226 flowers × Bedford Prolific (Group I), 0 fruit set. 23 flowers × Black Eagle (Group I), 0 fruit set. 140 flowers × Knight's Early Black (Group I), 0 fruit set. (Bottom of tree) 82 flowers × Late Black Big., 29 fruits set. 25 flowers × Waterloo, 14 fruits set. 60 flowers × Governor Wood, 19 fruits set. 43 flowers × Early Purple Gean, 20 fruits set. 97 flowers × Big. Noir de Schmidt, 43 fruits set. 75 flowers × Guigne de Winkler, 18 fruits set. A few of the matured fruits had fallen from this tree before it was photographed.

Fig. 2. Guigne de Winkler (Group II). (Left-hand side) 115 flowers self-pollinated, 0 fruit set. 88 flowers × Big. de Schrecken (Group II), 0 fruit set. 73 flowers × Big. Frogmore (Group II), 0 fruit set. (Right-hand side) 60 flowers × Bedford Prolific (Group I), 44 fruits set. 10 flowers × Knight's Early Black (Group I), 8 fruits set. 36 flowers × Big. Napoleon (Group III), 26 fruits set. 17 flowers × Emperor Francis (Group III), 14 fruits set. 49 flowers × Governor Wood, 23 fruits set.

Fig. 3. Big. Napoleon (Group III). (Left-hand side) 184 flowers self-pollinated, 0 fruit set. (At top of tree) 337 flowers × Emperor Francis (Group III), 0 fruit set. (Centre and right-hand side) 31 flowers × Empress Eugenie, 24 fruits set. 109 flowers × Late Black Big., 51 fruits set. 19 flowers × Guigne de Winkler (Group II), 6 fruits set. 80 flowers × Big. de Schrecken, 46 fruits set. 38 flowers × Knight's Early Black (Group I), 24 fruits set.

Fig. 4. President (Group III). (Left-hand side) 54 flowers × White Magnum Bonum, 42 fruits set. 52 flowers self-pollinated, 0 fruit set. (Right-hand side) 30 flowers × Late Orange (Group III), 0 fruit set. 50 flowers × Coe's Golden Drop (Group I), 42 fruits set.

Fig. 5. Cambridge Gage (Group III). (On left-hand side) 791 flowers self-pollinated, 23 fruits set. (On right-hand side) 203 flowers × Coe's Violet (Group I), 109 fruits set. 242 flowers × Late Orange (Group III), 9 fruits set.

BLUE ROCK

Fig. 6. Blue Rock (Group IV). (On left-hand side) 356 flowers self-pollinated, 3 fruits set. (At top of tree) 154 flowers × Rivers' Early Prolific (Group IV), 3 fruits set. (On right-hand side) 126 flowers × Coe's Violet (Group I), 96 fruits set. 103 flowers × Late Orange (Group III), 66 fruits set.

GENETIC AND CYTOLOGICAL STUDIES IN WHEAT. II.

By A. E. WATKINS, M.A.

Plant Breeding Institute, Cambridge.

CONTENTS.

INTRODUCTION.

THE reduction divisions in the microspore mother cells of hybrids between *T. turgidum* with 28 chromosomes and *T. vulgare* with 42, and the chromosome composition of the progeny therefrom, have already been described (1). From the discussion of the results obtained, it is clear that an accurate knowledge of reduction in the megaspore mother cell, of the development of the embryo-sac, fertilisation, germination of the grain, and related problems, is of cardinal importance: in the present paper it is proposed to give the information so far obtained on these points.

MATERIAL.

The parent varieties used were:

T. turgidum, var. *iodurum*, Körn., "Rivet." 28 chromosomes.

T. vulgare, var. *lutescens*, Körn., "Yeoman." 42 chromosomes.

T. vulgare, var. *albidum*, Körn., "Swedish Iron." 42 chromosomes.

Material for the description of reduction in the megaspore mother cell was provided by plants of the F_3 generation of Rivet ♀ × Yeoman ♂; by F_1 plants from Rivet ♀ × Iron ♂; and by some of the plants used to describe reduction in the microspore mother cells. The development of the embryo-sac, and fertilisation, is described for F_3 plants from

Rivet ♀ × Yeoman ♂. All the plants used were known to have univalent chromosomes, and were partially sterile.

The material for the tests of grain germination, and of pollen germination, are given later.

The Reduction Divisions in the Megaspore Mother Cells.

Reduction in the microspore mother cells in the genus *Rosa*, which is in many instances similar to that already described for wheat hybrids, does not always follow the same course as in the megaspore mother cells (2). It is therefore important to be sure that in wheat the behaviour is the same in the two cases; more especially, seeing that the observed absence of certain chromosome combinations in the progeny could readily be explained if this were not the case.

Stages from the heterotype prophase to the first division of the megaspore were found in ears prepared, primarily, for a study of reduction in the microspore mother cells; for these Carnoy's fluid was used as fixative, and the slides were stained in iron alum haematoxylin. In a few cases, preparations showing the row of four megaspores, or stages near thereto, were obtained from flowers fixed in Bouin's fluid to examine the development of pollen grains from microspores. Sections were cut at thicknesses from 12 μ to 14 μ.

Figs. 1–6 clearly show a behaviour of the chromosomes similar to that described for the microspore mother cells; but, to be certain that the frequencies of the classes of female gametes do not differ greatly from those calculated for the male gametes, a critical investigation of certain special points is necessary. First, reduction may not always follow the same course; secondly, the frequency of chromosome loss may not be the same in the female as in the male; thirdly, degeneration of three of the cells of the tetrad may be selective.

Study of reduction in the megaspore mother cells is rendered difficult by the fact that a single spike will probably not show more than a dozen ovules at any of the desired stages; so that the labour involved in obtaining an adequate amount of evidence would be very great. Nevertheless, though the data to hand is not very extensive, it will, I think, be found sufficient for our present purpose.

Out of 16 heterotype metaphases, 15 showed univalents quite clearly; and there was no suggestion that pairing did not take place in exactly the way already given in the description of microspore development. This is confirmed by the fact that the three heterotype anaphases discovered all show splitting univalents; but it is regrettable that so few

examples of this critical stage have been seen. Five out of the six instances, in which reduction was found to be at a stage from heterotype telophase to homotype prophase, show lost chromosomes; but there is not sufficient evidence to show that these occur with the same frequency as in microspore development. As far as the heterotype division is concerned, therefore, it seems probable that behaviour is the same in the two cases.

Some stages in the homotype division are shown in Figs. 5 and 6. The plane of division of the outermost cell may be parallel with (Fig. 5), or at right angles to (Fig. 6), that of its sister cell: that of the latter being always parallel to the plane of the heterotype division. Homotype anaphase has only been observed in a few cases, and then only in the outer daughter cell; here the univalents can be seen to segregate at random, and it is unlikely that the division of the inner cell would follow a different course—a conclusion that later evidence confirms.

It seemed possible that the degeneration of three of the cells of the tetrad (Figs. 7–9) might be selective with respect to their chromosome content; but this is not the case. For 32 observations show that it is always the three outer cells that degenerate; so that degeneration of the cells is clearly dependent solely on their position.

Knowing, then, that it is only the innermost megaspore that functions, it becomes important to know what chromosomes it has received; so counts have been made of the frequency of lost chromosomes at the 4-cell stage, and in the innermost megaspore after degeneration of the other three. Table I gives the result of a composite count, obtained from

TABLE I.

(a) *Compiled from various plants: not including plants S 6–9 and S 6–10, from which Tables II, III and IV were obtained.*

	1st and 2nd cells		3rd cell		4th cell	
No. of lost chromosomes	No. of cells	Propn. of cells	No. of cells	Propn. of cells	No. of cells	Propn. of cells
0	14	0·44	6	0·35	7	0·41
1	11	0·34	5	0·29	8	0·47
2	6	0·19	4	0·24	2	0·12
3	1	0·03	1	0·06	0	0·00
4	0	0·00	1	0·06	0	0·00

(b) *Proportions for 3rd and 4th cells, if plant S 6–10 is included.*

No. of lost chromosomes	3rd cell	4th cell
0	0·38	0·42
1	0·35	0·45
2	0·17	0·09
3	0·08	0·03
4	0·03	0·00

seven different plants. The count being made to determine whether loss of chromosomes affects all four cells equally, the fact that loss frequencies will differ in different plants will not matter so long as all four cells of each tetrad contribute an observation. In point of fact, the observations from the two inner cells were included in one instance where no reliable data could be obtained from the outer cells, but the error so introduced is not significant.

The two outermost cells are spoken of as the first and second cells; the innermost but one, as the third cell; and the innermost as the fourth cell.

The results show very close agreement between loss in the two outer cells on the one hand, and in the two inner cells on the other; but suggest—though errors from sampling alone are too great for this conclusion to be at all certain—that the loss from the third cell may be rather greater than from the fourth: a conclusion that is also suggested by the results given in Table III (*b*). This at first gave rise to some suspicion; but, upon consideration, it appears that such a result would be expected, as a consequence of the fact that the plane of the homotype division is parallel to that of the heterotype. For, the univalents lost at the heterotype from the inner daughter nucleus will tend to remain on the outer, micropylar, side of that nucleus; so that after the homotype division, they will be contained in the third cell of the tetrad—whether they become regained and are included by the nucleus, or are left free in the cytoplasm. It follows that the chance ("*m*," p. 147 of my former paper) that a univalent chromosome lost at the heterotype will be reincluded by the nucleus of the innermost megaspore, is probably zero. In plants A and B (1) this reduces the chance that any one univalent will be included within the nucleus of the innermost megaspore from 0·24 and 0·33 respectively, the values found for the microspores ((1) Tables I (*h*) and II (*p*)), to 0·12 and 0·29.

In Tables II (*b*), (*c*) and III (*a*), (*b*) a comparison is made, for two different plants, of the frequency of lost chromosomes in megaspores and microspores respectively; while in Table IV the results for the two plants are added together for further comparison.

The tables show, on the whole, fairly good agreement; and I think we can conclude that loss of chromosomes occurs with about the same frequency in megaspore formation as in microspore formation, though perhaps the number of observations is too few for a very definite conclusion. The agreement also seems to me to provide confirmatory evidence that in the homotype division of the megaspore mother cell the univalents segregate at random.

TABLE II.

Plant S 6–9.

(a) *Homotype loss at microspore formation.*

Two counts, made from two different flowers.

No. of lost chromosomes	No. of cells (1)	No. of cells (2)	Propn. of cells (1)	Propn. of cells (2)
0	11	30	0·52	0·53
1	6	19	0·29	0·33
2	3	7	0·14	0·12
3	1	0	0·05	0·00
4	0	1	0·00	0·02

(b) *Present in tetrads of microspores.*

No. of lost chromosomes	No. of cells (1)	No. of cells (2)	Propn. of cells (1)	Propn. of cells (2)	Total propn.
0	23	28	0·46	0·54	0·50
1	19	18	0·38	0·35	0·36
2	6	6	0·12	0·11	0·12
3	2	0	0·04	0·00	0·02
4	0	0	0·00	0·00	0·00

(c) *Present in innermost megaspore.*

No. of lost chromosomes	No. of cells	Propn. of cells
0	4	0·57
1	2	0·29
2	1	0·14
3	0	0·00
4	0	0·00

TABLE III.

Plant S 6–10 (37 chromosomes).

(a) *Tetrads of microspores.*

Two counts, made from two different flowers.

No. of lost chromosomes	No. of cells (1)	No. of cells (2)	Propn. of cells (1)	Propn. of cells (2)	Total propn.
0	18	21	0·36	0·42	0·39
1	21	25	0·42	0·50	0·46
2	10	3	0·20	0·06	0·13
3	1	1	0·02	0·02	0·02

(b) *Megaspores.*

No. of lost chromosomes	4th cell: No. of cells	4th cell: Propn. of cells	3rd cell: No. of cells	3rd cell: Propn. of cells	3rd and 4th cells: Total no.	3rd and 4th cells: Total propn.
0	7	0·44	4	0·40	11	0·42
1	7	0·44	4	0·40	11	0·42
2	1	0·06	1	0·10	2	0·08
3	1	0·06	1	0·10	2	0·08

TABLE IV.

Plants S 6–9 and S 6–10.

(a) *Tetrads of microspores.*

The results from the two plants are here added together.

No. of lost chromosomes	Propn. of cells
0	0·44
1	0·46
2	0·08
3	0·02

(b) *Megaspores.*

No. of lost chromosomes	3rd and 4th cells: No. of cells	3rd and 4th cells: Propn. of cells	Expected no. of cells, from (*a*)
0	15	0·46	14·5
1	13	0·39	15·2
2	3	0·09	2·6
3	2	0·06	0·67

It should be mentioned that the individual counts were made at such intervals of time—several months in some cases—that in every case the results of the previous counts were no longer remembered. Such a procedure is important, as the observations are often difficult to make with accuracy, and it would otherwise be impossible to avoid the suspicion that the agreement was due to an unconscious effort of the observer.

It will be seen that separate counts are given, in Tables II (*a*), (*b*), and III (*a*), for microspores from different flowers of the same ear. These also were made at varying intervals of time, to provide evidence for the constancy of chromosome loss in the different flowers. Agreement is good, except in Table III (*a*); and even here the form of the distributions is the same, and markedly different from that of Table II (*b*), which gives the results for the same stage in a different plant. The discrepancy may well be due to the difficulty of making accurate observations in microspores, where vacuolated lost chromosomes are sometimes difficult to detect. The results show, I think, that loss of chromosomes occurs with considerable regularity; but attention must be called to the fact that, in every case—and this applies both to megaspores and to microspores—the various counts, in each plant, were obtained from the same ear. Hence, as it was the constant practice to fix a whole ear at once, it follows that in the flowers compared reduction took place at the same time; and therefore, as nearly as can be, under the same conditions. It is possible that at different temperatures, for example, loss of chromosomes at reduction takes place with widely differing frequencies in different flowers of the same plant.

It is concluded that reduction follows essentially the same course in megaspore as in microspore mother cells, and that chromosomes are lost with about the same frequency in the two cases. But, since the planes of the heterotype and homotype divisions are parallel, the chance that any one univalent chromosome will be included by the nucleus of the innermost megaspore may, in some plants, be considerably less than the chance of its inclusion in a microspore nucleus.

THE DEVELOPMENT OF THE EMBRYO-SAC, AND FERTILISATION.

The development of the embryo-sac from the megaspore has not been described for wheat, so far as I am aware; but fertilisation, from shortly after the entrance of the pollen tube to the end of the first division of the fertilised egg-cell, has been described by Sax (3). It will therefore be necessary to give an account of the normal course of development, and then to show what deviations therefrom are found in those ovules that fail to produce grain.

Material showing the development of the embryo-sac, as far as the stage of Fig. 11, was fixed in Bouin's fluid. Material for stages from that of Fig. 12 up to, and including, fertilisation was fixed in Bouin's fluid or in Flemming's stronger solution. The latter fluid was also used for fixing ovaries from ears that had already flowered.

The innermost megaspore enlarges (Fig. 9), and divides to form the two-celled embryo-sac. The next stage observed is the eight-celled sac of Fig. 10, where the egg-cell, one of the synergids, the approaching polar nuclei, and two of the antipodals, will be seen. The latter are here present as cells with small, undifferentiated, nuclei. As development proceeds they increase in size, and continue to divide until some 20 or so are present—division ceasing shortly after the stage of Fig. 11. The general character of the changes undergone by the nuclei of the antipodal cells is shown in Figs. 10–13, and it will be enough here to point out the main features. Throughout, the cytoplasm is very dense and there are no cell walls; the nuclei enlarge enormously; and the nucleolus, besides enlarging, becomes very irregular in shape. The reticulum is at first (Fig. 10) that of a typical nucleus, but later (Figs. 12–13) becomes less and less so, until it is finally (Fig. 13 *d*) represented as a very dense and irregular mass of rather indistinct threads, which do not appear to be clearly set apart from the surrounding cytoplasm.

The development of the polar nuclei is shown with sufficient accuracy by the figures (Figs. 10–13). They remain, surrounded by cytoplasm,

just below the egg-cell, in very close contact; but do not fuse until the arrival of the second male gamete.

The distinction between the egg-cell and the synergids appears at about the stage of Fig. 11. The nucleus of the former has, at first, the structure of a typical resting nucleus; later the threads of the network become more distinctly granular (Fig. 12), and finally (Fig. 13 *b*) seem to take on the structure of threads with short fine branches. At this final stage, the threads are only few in number, so that the nucleus has a markedly transparent appearance. As shown in Fig. 12, the cytoplasm is now densest round the nucleus, and somewhat vacuolated round the lower part of the periphery; but this change is not constant, and the process is rather irregular.

Figs. 10, 11, 12 *b*, and 13 *b* show the development of the synergids. They finally become pear-shaped, each with an inconspicuous bun-shaped nucleus near the periphery, with cytoplasm almost uniform but slightly denser at the micropylar end; and often contain one or two small patches or globules of material (*g*, Fig. 12 *b*) which appear almost homogeneous, and stain only slightly more densely than the cytoplasm.

An attempt has been made, in the figures, to show the relative densities of the cytoplasm in the different regions of the embryo-sac.

Figs. 10–12 and 13 *b*–*d* are drawn to the same magnification, 520 diameters, while the magnification of Fig. 13 *a* is 230 diameters. They show the increase in size of the embryo-sac; and that after the stage of Fig. 12 enlargement takes place chiefly in the size of the cavity itself —except in the case of the antipodals, which increase in size enormously throughout. Though Fig. 13 represents the final stage of development, fertilisation may occur (Fig. 14) at about the stage of Fig. 12.

I have not been able, so far, to observe the entry of the pollen tube into the micropyle; but its presence is made evident, soon afterwards, by the fact that the synergid which it attacks stains very densely indeed —so much so, that its contents are very difficult to make out, and it has not yet been found possible to trace the stages that follow, until the time when the two male gametes can be clearly seen outside the egg-cell and the polar nuclei respectively (Figs. 15 *a* and 15 *c*). By this time, a mass of darkly staining granules has appeared in the neighbourhood of the egg-cell. Their mode of origin is uncertain: often they seem to issue from the attacked synergid (Fig. 15 *b*) and form a ring round the egg-cell; but at other times appearances suggest that they are formed by the coagulation of the strands of cytoplasm surrounding the egg-cell.

After fertilisation the unattacked synergid rapidly degenerates; but

the other one remains, for some considerable period, as a uniform densely staining mass.

The fusion of the male gametes with the egg-cell and polar nuclei respectively, and the first division of the fertilised egg-cell and the triple fusion nucleus, have been described by Sax (3). My own observations are in agreement, so it will suffice to give a few figures (Figs. 16–17).

The endosperm characters in wheat are strictly maternal in their inheritance (4, 5), so that the question of triple fusion is one of some importance. The figures of Jensen (6), who first reported it for wheat, are very inadequate; but more recently Sax (3) has shown clearly that it does occur. I have observed it several times myself, and it probably is, in fact, the rule—but this, of course, cannot be stated definitely. However, there is so far no evidence that the endosperm ever develops without triple fusion; and Percival's statement (7), that he has observed the second male gamete still within the pollen tube in cases where endosperm cells are present must be accepted with considerable reserve; for, after penetration by the pollen tube, the synergid disorganises, and often contains small masses of densely staining material, one of which might perhaps be mistaken for a male gamete (see, for example, Fig. 16 *b*).

In a small proportion of cases ovules, from ears at the time of flowering, have been found devoid of contents or with traces of degenerate tissue. At what time this degeneration happens is not known; but the evidence to hand suggests that it occurs early in the development of the embryo-sac and not shortly before fertilisation; for it is doubtful whether anything likely to correspond to a stage in degeneration has been seen. This is clearly one cause of failure to set grain; but Table V shows that, numerically, it is not a very important one.

TABLE V.

No. of plant	No. of embryo-sacs studied	No. of aborted embryo-sacs	Propn. of aborted embryo-sacs	Propn.* of sterile flowers
S 6–7	26	4	0·15	0·68
8	35	2	0·06	0·37
9	29	3	0·10	0·32
10	21	0	0·00	0·73

* The proportion of grains in the first (bottom) two flowers of each spikelet was measured.

In one instance, an embryo-sac containing antipodals, two polar nuclei in contact, three synergids, and two egg-cells, was noticed. The manner of its origin is not known.

In the plants studied, about 92 per cent. of the embryo-sacs, from

ears in which flowering was just beginning, appear to be quite normal. Little more than half these become fertilised, however; and the question at once arises whether this is due to an insufficiency of functional pollen, or to the fact that some morphologically perfect egg-cells are unable to function. The course of degeneration in these embryo-sacs need not be described in detail. It will suffice to mention that the polar nuclei and the synergids probably begin to degenerate first, and the egg-cells and antipodals later; but this sequence may not be invariable. Such ovaries are found at harvest as dry, shrivelled, structures, some 1 or 2 mm. long[1].

After fertilisation the fusion nucleus divides rapidly—it completes about four successive divisions by the time the fertilised egg-cell has reached the metaphase of its first division—and the nuclei so formed lie scattered in the cytoplasm which lines the cavity of the embryo-sac. Until a late stage in the development of the grain all the endosperm nuclei divide simultaneously—the increase in their number keeping pace with the increase in size of the ovary; and, as growth proceeds, the antipodals become absorbed and disappear. Throughout development, as far as studied, the divisions of the endosperm nuclei are quite normal.

The fertilised egg-cell divides normally (Fig. 17); and few abnormalities in embryo development have been noticed as far as my observations go —that is, to stages in which the embryo is about 100-celled, and the young grains quite large. This is confirmed by the fact that at harvest there is no intermediate stage between structures that are clearly grains—albeit they are small and shrivelled—and the shrivelled ovaries, in which fertilisation did not take place, from the sterile flowers.

It remains to consider cases of abnormal development after the entrance of the pollen tube into the embryo-sac. They are four in number: that is, about 5 per cent. of the 77 ovaries studied.

The first is shown in Fig. 18, and is difficult to interpret otherwise than as degenerating egg-cell, synergids and pollen tube. If we accept this we can conclude almost certainly—both from the condition of the egg-cell and the polar nuclei, and more certainly from the fact that the synergids are both untouched by the pollen tube—that fertilisation has not taken place. The hypothesis that I most favour is that the pollen tube arrived so late that the egg-cell had already begun to degenerate, and so could not be fertilised: a view which, as will be seen later, has at any rate the advantage of bringing the case into line with other observa-

[1] Frederikse (23) reports that, in several animals, egg-cells that are not fertilised show rudimentary parthenogenesis. In wheat, neither the egg-cell nor the polar nuclei show any tendency whatever to divide, but simply degenerate.

tions. It is true that this suggestion requires us to believe that a degenerating egg-cell is still able to attract a pollen tube; but if the egg-cell were non-functional for other reasons, or if the fault lay with the pollen tube, or with the male gametes, we should still have a similar difficulty.

Fig. 20 *a* shows a fairly large and apparently normal embryo, and by it the remains of the synergid that was attacked by the pollen tube; while in Fig. 20 *b* we see the polar nuclei, obviously not fertilised, from the same embryo-sac. All the tissue of the ovule and ovary is quite sound, and there are not yet any signs of abnormality in the embryo—indeed one of the cells is in the early telophase of division. Perhaps we have here a case in which the pollen tube arrived late: at a time when the polar nuclei had begun to degenerate, but the egg-cell was still sound. But it may equally well be that the pollen tube arrived with only one male gamete.

Figs. 19 and 21 both show ovaries, in which development has gone on normally for some time after fertilisation, beginning to degenerate. In both, the tissue of the ovary and ovule is dead or degenerating and the embryo is beginning to abort. In the first, the endosperm nuclei are present only as a mass of chromatic granules, surrounding a nucleolus and lying free in the cytoplasm; in the second, a considerable amount of endosperm has been formed, but all of it has degenerated. In the present season (1924) similar occurrences have been found to result from the ravages of larvae of the wheat midge, *Cecidomyia tritici*, and it is probable that all cases of the degeneration of a fertilised ovary are to be attributed to this cause.

The approximate proportion[1] of cases in which the various types of behaviour occur (the mean values for the plants investigated) are as follows:

Aborted, non-functional, embryo-sacs (1)		0·08
Apparently normal embryo-sacs	(2) not fertilised	0·43
	(3) fertilised and develop normally	0·48
	(4) abnormal, but doubtful interpretation	0·01
Mean proportion[1] of grains obtained from the same plants		0·50

Grains may be expected to develop from class 3. The proportion given for this class is probably an under-estimate; as a few ovaries, in which the size and general appearance indicated normal development after fertilisation, were not cut up. However, the agreement between this proportion and the proportion of grains obtained is good.

[1] For the cytological work, only ovaries from the first two flowers of each spikelet were used. The proportions here given are therefore strictly comparable with the proportion given for the grains obtained (see previous note, p. 331).

To sum up: Only a small proportion of embryo-sacs are obviously non-functional, and failure to set grain arises, principally, from the fact that many morphologically perfect egg-cells are not fertilised. After fertilisation, development proceeds normally, with rare exceptions.

The Grains and their Germination.

In the first paper of this series (1), one of the three hypotheses, put forward to account for the non-appearance of certain expected chromosome combinations, was that such combinations produced non-viable embryos or plants which died while still young. With the object of testing this hypothesis it was determined to carry out a series of germination tests. In describing these experiments, the grains produced as the immediate result of a cross—therefore those which on germination will produce the F_1 plants—will be referred to as F_1 grains; those borne on the F_1 plants will be referred to as F_2 grains, and so on.

The F_1, and nearly all F_2 grains, from crosses between species of wheat that differ in chromosome number, are wrinkled and badly filled; in this way contrasting sharply with the plump, well-filled grains produced by pure lines and by other crosses. This wrinkling is indeed found in most of the grains from partially sterile plants of later generations as well. F_1 grains, for instance, swell during development to a size much greater than that of a normal grain; but seem to contain a percentage of dry matter below the normal, for during ripening—a process mainly involving loss of water—they shrink in volume more than the average grain, and finally become wrinkled.

F_1 grains are always wrinkled; but those obtained when *vulgare* is the female parent are less wrinkled than the grains from the reciprocal cross. F_2 grains show all gradations between very wrinkled and not wrinkled. Both have a marked tendency to germinate while still in the ear; they may show signs of attack by fungus; and are often discoloured —sometimes as the result of the depredations of the larvae of the wheat midge. In these particulars, conditions during ripening probably have a large effect; for grains from the 1923 harvest were in better condition than those of the previous year.

In the sterile flowers which do not produce grain, the ovary at the time of harvest is a shrivelled structure, 1 or 2 mm. long. There is no possibility of confusing these structures with ovaries that have been fertilised. Occasionally the latter may be attacked by *Cecidomyia* larvae so soon after fertilisation that they never develop properly, but even then they are distinctly larger than the unfertilised ovaries and show

some of the characters of a grain. With these exceptions, fertilised ovaries always develop into structures that are clearly grains, however small and shrivelled they may be. It is clear, therefore, both from these observations and from the cytological work, that a grain germination test, and observations on the number of young plants that die, will show us all the non-viable zygotes.

In carrying out these tests, two objects had to be kept in view: one to provide conditions for germination both good and constant; the other to provide good conditions for the growth of the young plants. Field conditions clearly will not admit of an accurate germination test, and in addition leave the plants open to attack by wireworm. On the other hand, field conditions are probably the best for plants that are once established: if grown under glass, for instance, they are often attacked severely by mildew and other organisms; and growth is always checked unless there is ample root room. After due consideration of these and other difficulties, the method adopted was to sow each seed about half an inch deep in a "T. P. Raiser[1]," containing a mixture of three parts of pure sand to one part of baked earth. They were then kept in a moderately warm room and watered regularly—keeping all equally moist as far as possible. A few days after the shoot was seen above the surface of the compost, the young plant was transferred by degrees to the open; and, shortly after the first foliage leaf had emerged from the coleoptile, were transplanted into one of the field cages. Each box was numbered; and the dates of planting, emergence of the coleoptile, transplanting, and so on, were noted. The plants were examined at intervals during their growth.

F_2 grains from the cross Rivet × Iron, and grains from 10 F_2 and 10 F_3 plants of the cross Rivet × Yeoman comprised the bulk of the material. Of the latter (plants S 6–1 to S 6–10 of Table VI), it may be stated here that inspection of their characters showed that all had more than 35 chromosomes; furthermore, all except numbers S 6–1 and S 6–3 were partially sterile, and I have little doubt that this means that they had less than 42 chromosomes. The remainder of the material consisted of grains from the pure lines Rivet and Benefactor (*T. vulgare*), and F_1 grains from a number of crosses which it was thought might be useful for comparison.

In all, 709 grains were sown. Sowing occupied a period from Nov. 1st to Nov. 25th, 1923; and transplanting from Nov. 16th to Dec. 19th, 1923.

The results are given in Tables VI *a* and VI *b*.

[1] A "T. P. Raiser" is a cardboard box, about 1½ inches cube, with no top, and a detachable bottom.

TABLE VI *a*.

Description of grain	No. sown	No. germd.	No. plants trans-planted	No. plants survived	Plants survived/grains sown
Benefactor	13	13	13	13	1·00
Rivet	13	13	13	13	1·00
T. vulg. × *T. turg.* F_1	10	10	10	10	1·00
Progeny of S 6–1	32	32	32	32	1·00
,, S 6–3	32	32	32	31	0·97
,, S 22 F_1	8	7	6	5	0·62

S 6 = Rivet ♀ × Yeoman ♂. Plants 1 to 10 of this series were F_3 plants.
S 22 = (Rivet × Iron) 42 chromosome segregate ♀ × Rivet ♂.

TABLE VI *b*.

Description of grain	No. sown	No. germd.	No. plants trans-planted	No. plants survived	Plants survived/grains sown
Progeny of S 6–2	7	7	7	7	1·00
,, S 6–4	9	9	9	6	0·67
,, 5	32	32	32	29	0·91
,, 6	32	32	31	31	0·97
,, 7	16	11	9	5	0·31
,, 8	32	32	31	24	0·75
,, 9	31	31	30	27	0·87
,, 10	28	23	23	20	0·71
,, T 45–1	32	30	27	19	0·59
,, 2	32	31	24	22	0·69
,, 3	32	28	25	19	0·59
,, 4	32	31	30	30	0·94
,, 5	32	32	32	32	1·00
,, 6	32	25	25	25	0·78
,, 8	19	16	15	14	0·74
,, 9	5	5	5	5	1·00
,, 10	3	3	3	3	1·00
,, 11	32	30	30	29	0·91
,, plant B	33	23	23	22	0·67
Rivet × Iron F_2	45	41	40	37	0·82

T 45 = Rivet ♀ × Yeoman ♂. Plants 1 to 11 were F_2.
Plant B is Plant B of my former paper; expected non-viability was about 90 %.

The success of the method is shown (Table VI *a*) by the fact that the 10 F_1 grains from Iron by Rivet, the 26 grains from the pure strains, and the 64 grains from the fully fertile F_3 segregates, all germinated; and, with one exception, gave plants which ripened grain. The relative failure of grains from S 22 F_1 probably shows the uncertain nature of the grains themselves, rather than any uncertainty in the method; and, as the grains are genetically identical, it makes it doubtful whether we are justified in regarding the failure of some of the grains of later generations as necessarily due to a specific non-viability, instead of to mere fluctuations in development and ripening.

Turning now to Table VI *b*, we find that an appreciable number of

grains failed to give mature plants; and this is due, partly to failure to germinate, and partly to the death of the young plants. It will be recalled, however, that in plant B the expected proportion of non-viable progeny —on the theory of random mating between gametes of the same class frequencies—was about 0·91: the proportion found is 0·33. Indeed, throughout the table, we find a surprisingly high survival rate: high enough to leave very little doubt, even without a knowledge of the chromosome number of the various plants tested, that the theory proposed is incorrect. This conclusion is amply borne out by a fuller consideration of the data. Plant S 6–10 has 37 chromosomes; in plants S 6–6, 7, and 9, the chromosomes have not been counted accurately, but a preliminary examination shows that the first two have not more than 39, and the latter not more than 38, chromosomes. If we assume that in all these cases the chance of any one univalent's being included in a microspore nucleus is 0·45, the theory of random mating gives the following results:

No. of plant	Expected propn. of non-viability	Propn. of seeds not giving plants that completed development (from Table VI *b*)
S 6–6	0·65	0·03
7	0·65	0·69
9	0·76	0·13
10	0·84	0·29

Actually, it is unlikely that the chance of a univalent's inclusion in a microspore, or megaspore, nucleus would be as high as 0·45; and if the chance were less, the proportion of non-viability would be increased[1].

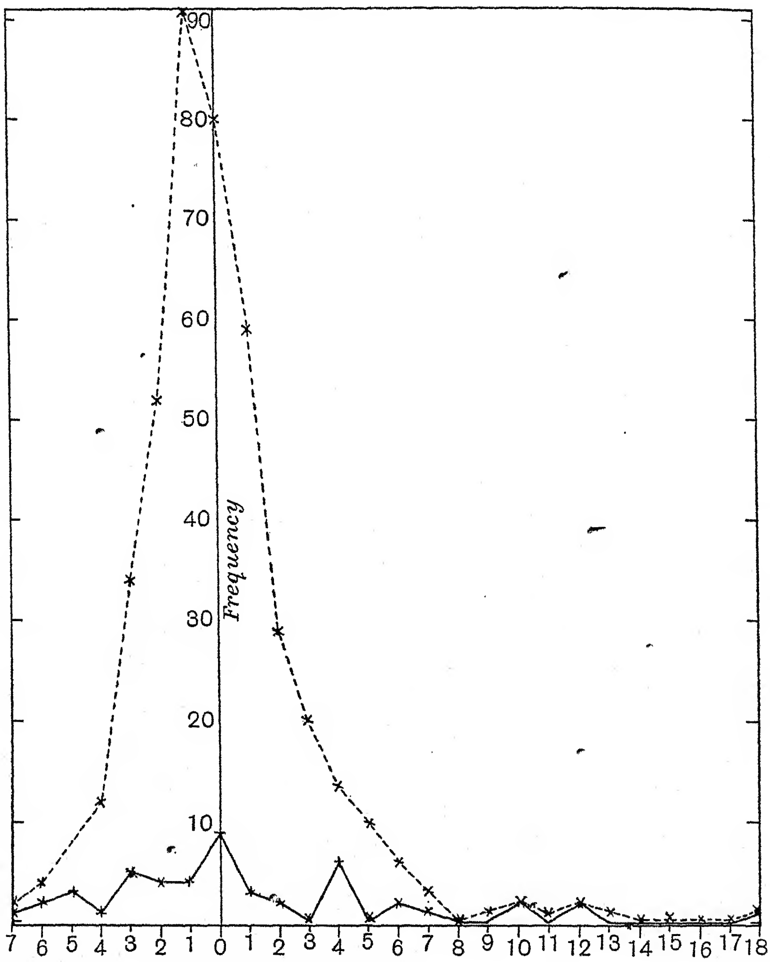
These results admit of no mistake; nor is there any doubt that the discrepancy between observed and expected proportions cannot be accounted for by the cases (p. 332 onwards) in which development becomes abnormal shortly after the entrance of the pollen tube.

There remain, broadly speaking, two possibilities. One is that only male gametes with 14 or 21 chromosomes effect fertilisation, and that non-viability has no connection with the absence of some of the expected chromosome combinations. The second is that the early death of embryos, the failure of grains to germinate, and the failure of plants to complete development, represent, in whole or in part, the elimination of the zygotes that are not found; but that such eventualities do not occur in the expected proportions, through there being a greater chance that fertilisation is effected by male gametes with 14 or 21 chromosomes than

[1] In a plant with more than 35 chromosomes, the fact that "*m*" probably equals 0 in megaspore development would increase the amount of non-viability.

by those with an intermediate number. The latter theory is the more probable.

If the second of these two hypotheses be correct, then all zygotes obtained by crossing the F_1 back to either of the parents should be viable;



Text-fig. *a*. Deviation from mean number of days from sowing to germination.

while, according to the first, they need not be. A surer, if more difficult, test can be obtained by germinating grains from plants with known chromosome numbers, and counting the chromosomes in the root tips.

For if any of the offspring of a plant with 37 chromosomes, for example, had fewer than 37 chromosomes, it would (1, p, 152) represent one of the non-viable combinations; and it is possible that examination of a large number of root tips would reveal whether such zygotes exist.

With the object of testing the first hypothesis, both parents have been pollinated with F_1 pollen. The grains obtained should, if only male gametes with 14 or 21 chromosomes function, give plants with 28, 35 or 42 chromosomes.

Before concluding this section, some more of the data obtained from the germination tests will be mentioned briefly. Text-fig. *a* shows the irregularity with which the grains germinated; and indicates that there is a tendency for grains that were long in germinating to give plants that subsequently died. Those that had not produced a visible shoot by Dec. 19th—that is, from 28 to 45 days after sowing—were counted as not having germinated, and were dug up and examined. Some had not begun to germinate; some had germinated improperly (giving, for instance, a shoot and no roots, or *vice versa*); others had given small roots and shoots in various stages of development. The mean number of days required for germination was about 13.

The results show no significant variation between different tillers of the same plant.

Death of the plants might occur at any time after germination. In most cases it happened before reduction, but sometimes development would cease just after the time when, judging by the appearance of the plant, reduction had taken place; sometimes, again, it ceased just before the ear emerged from the sheathing leaves; and, finally, sterile plants in which the ear had emerged a short way would seem to complete the series. The observations so far made suggest, in fact, that a continuous series might be traced between grains that do not germinate and plants that ripen grain.

In Text-fig. *a* the deviations of the number of days taken by a grain to germinate are not measured from a common mean, but from the means for the progeny of the respective plants.

POLLEN GERMINATION AND POLLEN TUBE GROWTH.

The previous considerations leave little doubt that much light on the problem we are considering will be thrown by a study of the germination of the pollen grains, and the growth of the pollen tubes.

It is difficult to germinate wheat pollen artificially, but germination can be brought about if the grains are kept in an atmosphere containing

the right amount of moisture: if the atmosphere be too dry the grains collapse; if it be too moist they swell and burst. Firbas (8) has obtained fairly good results by scattering the grains on a slide, and breathing on them for a minute or so. Apart from the unreliability of the method, however, and from the fact that it is not possible, in this way, to induce the tubes to grow to a length greater than the diameter of the pollen grain, it is clear that in the present case a more accurate knowledge of the facts would be obtained by observations carried out on the stigmas of the plants we are considering, at various intervals after pollination. Accordingly, this was the method employed.

In wheat there are two feathery stigmas inserted on the ovary. Each consists of a central tapering column, from which arise numerous fine, papillate branches, portions of which are outlined in Figs. 24–27. The form of the stigma therefore precludes measurement of the rate of pollen tube growth, by cutting transverse sections of the style at various distances from the stigma, and counting the number of pollen tubes present —a method used with success by East and Park in *Nicotiana* (9). It is possible, however, to measure the proportion of germination among the grains that fall on the stigma, and to trace the course followed by the pollen tube. To accomplish this it is clear that the ordinary methods of fixation and staining will not be accurate, as many grains would fall off the stigma; and it is necessary to mount the stigma direct in a fluid in which it can be examined—one that will act both as fixative and stain. A number of reagents were tried, but by far the most satisfactory was a dilute solution of cotton blue in lactic phenol[1]. This stain, as ordinarily used, is made up in the proportion of 0·5 gm. of cotton blue to 100 c.c. of lactic phenol; and, so made, it is necessary to differentiate in lactic phenol after staining. In the present instance, weaker solutions—0·10 gm. or 0·08 gm. to 100 c.c.—were used, and the results were quite satisfactory. The stigma is mounted direct in the fluid, without any difficulty being experienced from air bubbles, which were the source of much trouble with some other reagents that were otherwise satisfactory. The slides can be examined almost immediately after mounting. In some cases overstaining began after about 1 month, in others not until after 4 months. The reason for this difference is uncertain; but it is suggested that if the actual quantity of fluid, in which the stigma is mounted, is small, and is distributed in an even, thin film under the cover-slip, over-staining will not occur. There seems to be little difference between solutions containing 0·08 gm. and 0·10 gm. respectively of stain to 100 c.c. of lactic phenol;

[1] Lactic phenol consists of lactic acid, phenol, glycerine and water, in equal parts.

except that with the former a longer time, up to 3 or 4 days, may elapse before staining is sufficiently deep. Stronger solutions are not satisfactory, in my experience. The pollen tubes show up very clearly, and their passage through the branches of the stigma can be traced with ease. The disadvantage of the method is that it does not render visible the tube nucleus and the male gametes; but in view of its simplicity, and the length of time the preparations will keep, it should prove valuable for studying pollen germination in any plant in which the form of the style and stigma admits of its use.

When receptive the stigmas curve away from each other, but remain within the paleae. The anthers begin dehiscence from the tip, and some pollen is shed on the stigma; the filaments then increase rapidly in length, the paleae open slightly, and the anthers emerge from the flower and shed the remainder of their pollen into the air, unless, as sometimes happens, they get entrapped by the paleae. With rare exceptions, self-fertilisation always occurs in this country. Three circumstances probably contribute to this end: pollen is shed on the stigmas before the flower opens; the flower remains open for only a short time; and, lastly, wheat pollen does not remain viable for long after it is shed. To secure success in crossing, the stigma must of course be receptive, and pollen must be taken from the anther just as the latter dehisces: fine weather is absolutely essential. It is apparent that the same conditions are necessary in carrying out a germination test on the stigma; and care was taken to this end. But, at the same time, it is a matter of experience that perfect success is not attained in crossing, and we must therefore expect that a few of the tests will give incorrect results.

The tests were carried out at intervals from May 17th to July 14th, 1924. Good weather conditions obtained throughout, and the results from crosses made during the same period indicate that the data given by about 90 per cent. of the stigmas can probably be accepted as accurate. Stigmas were mounted at intervals of from 2 to 31 hours after pollination.

Preliminary observations were made on *T. vulgare*, var. "Chinese White," and Figs. 22–25 were drawn from this variety. The first sign of germination is the raising of the lid that closes the pore; the pollen tube emerges shortly afterwards. Well-developed tubes are shown in Figs. 24 and 25. The tube attains a considerable length before the pollen grain is emptied of its contents; and, after this, it dies down behind as the foremost end grows on: Fig. 26 shows the rear end of a tube that has reached this stage. The pollen grain is then, of course, left empty, so that, as time goes on, the proportion of empty grains on the stigma

increases continuously. Occasionally the tube may grow in the wrong direction—away from the central column instead of towards it. This may happen in a pure line (it has been noticed in Chinese White) as well as in hybrids, but it cannot yet be said whether it occurs with equal frequency in the different cases. Fig. 27 was drawn from a stigma of *vulgare* × *turgidum* F_1 pollinated by the *vulgare* parent. In Chinese White, about 4 per cent. of the grains had germinated after 4 hours from pollination, but in one or two cases a tube had reached a fair length by then—Fig. 25 shows one such case. The number of germinated grains increased continuously up to about 8 hours from pollination, by which time about 95 per cent. of them had germinated.

Upon examining slides showing the germination of pollen from *vulgare* × *turgidum* F_1, on the stigmas of the F_1 plants or on those of the parents, it is at once apparent that only a low proportion germinates —despite the fact that some 80 per cent. or so is morphologically perfect. Indeed, the small number of pollen tubes that can be seen leads one to suppose that only about 1 per cent. germinates; but measurement shows that, in general, about 10 per cent. is the true amount.

The germination of Rivet pollen on stigmas of Iron and (Iron ♀ × Rivet ♂) F_1, and of Iron pollen on the stigmas of Rivet and the aforesaid F_1, has been studied by counting the proportions of germinated grains at various intervals after pollination. On any stigma, the grains can be conveniently divided into six classes, as follows:

(1) The tip of the pollen tube has just protruded;
(2) a pollen tube has emerged;
(3) germination has not occurred;
(4) the grain has burst—an irregular mass of cytoplasm and starch grains being extruded;
(5) the grain has germinated, and extruded cytoplasm and starch grains as well;
(6) empty grains, including those that were devoid of contents when shed on the stigma, and those that were left empty by the growth of the pollen tube.

On different stigmas, the proportions of classes (4) and (5) added together varied from 0·01 to 0·11; the mean proportion for 12 stigmas being 0·05. These are not included in the tables.

Inaccuracy is probably introduced by the detachment of grains when the stigma is removed from the ovary and mounted. In some cases, too, the fact that the pore was on the under side of the grain made classification difficult; but the error from this source is not likely to be great.

For an accurate count to be made, the stigma must not be covered too thickly with pollen. In some cases part of a stigma had to be disregarded for this reason, but most counts were made from a complete stigma, and included the grains that had floated off into the fluid. The results are shown in Table VII.

TABLE VII.

(a) *Rivet ♂ on Iron ♀. Pollinated* 4. vii. 24.

Hours after pollination	3	4	$5\frac{3}{4}$	7
Tip protruded ...	0·05	0·07	0·04	0·18
Tube emerged ...	0·36	0·46	0·33	0·15
Empty	0·38*	0·33	0·41	0·18
Not germinated ...	0·20	0·14	0·22	0·49
Total no. grains ...	125	129	97	27

* A number of dwarf, empty grains were present, and the high proportion of empty grains probably means that the number of aborted grains was abnormally high.

(b) *Rivet ♂ on Iron ♀. Pollinated* 5. vii. 24.

Hours after pollination	3	$3\frac{3}{4}$	$5\frac{3}{4}$
Tip protruded ...	0·06	0·13	0·10
Tube emerged ...	0·09	0·36	0·30
Empty	0·17	0·27	0·12
Not germinated ...	0·68	0·24	0·48
Total no. grains ...	108	69	70

(c) *Iron ♂ on Rivet ♀. Pollinated* 5. vii. 24.

Hours after pollination	$4\frac{1}{4}$
Tip protruded ...	0·06
Tube emerged ...	0·41
Empty	0·23
Not germinated ...	0·30
Total no. grains ...	105

(d) *Rivet ♂ on (Iron × Rivet)* F_1 *♀. Pollinated* 4. vii. 24.

Hours after pollination	$3\frac{1}{4}$	$4\frac{1}{4}$	$7\frac{1}{4}$
Tip protruded ...	0·02	0·03	0·18
Tube emerged ...	0·62	0·40	0·10
Empty	0·29	0·54	0·38
Not germinated ...	0·07	0·03	0·34
Total no. grains ...	61	65	70

A slide made $5\frac{3}{4}$ hours after pollination showed a high proportion of germination, and no count was made.

(e) *Rivet ♂ on (Iron × Rivet)* F_1 *♀. Pollinated* 5. vii. 24.

Hours after pollination	$3\frac{1}{2}$	$4\frac{1}{2}$	$6\frac{3}{4}$
Tip protruded ...	0·16	0·01	0·11
Tube emerged ...	0·15	0·65	0·38
Empty	0·13	0·25	0·35
Not germinated ...	0·56	0·09	0·16
Total no. grains ...	123	78	62

(f) *Iron ♂ on (Iron × Rivet)* F_1 *♀. Pollinated* 27. vi. 24.

No distinction was made here between the first two classes.

Hours after pollination	$4\frac{1}{4}$	5	$6\frac{1}{4}$	$7\frac{1}{4}$	10
Germinated	0·23	0·54	0·95	0·93	0·48*
Empty	0·04	0·22			0·19
Not germinated ...	0·73	0·23	0·05	0·07	0·33
Total no. grains ...	273	151	175	153	88

* In addition to the fact that germination was low, many of the grains had only protruded the tip of the pollen tube.

In pure lines of wheat the proportion of aborted pollen grains varies from about 0·02 to 0·04; so that, except where a note to the contrary has been made, little error will be introduced by taking the total proportions of empty grains, given in Table VI, as grains that have germinated. In several cases the proportion of germinated grains was clearly much higher in some regions of the stigma than in others, which suggests that pollination was sometimes carried out before the stigma had reached its maximum receptiveness. This conclusion is confirmed by the fact, exemplified in (*a*) 7 hours, (*b*) $5\frac{3}{4}$ hours, (*d*) $7\frac{1}{4}$ hours, and (*f*) 10 hours, of Table VII, that the stigmas last taken often show a low proportion of germination. In wheat, flowering begins just above the middle of the ear and proceeds progressively from spikelet to spikelet passing up and down the spike. It was the practice to pollinate stigmas from part of the lower half of the ear and, generally, to mount first those from the top. This sequence was not invariable, but it seems quite likely that the less receptive stigmas were taken last; and it is difficult otherwise to account for the above-mentioned fact. The bulk of the evidence does not support the hypothesis that this results from the detachment of empty grains when removing the stigma. Considered as a whole, the results are not very consistent. Moreover, germination seems often to be more rapid than was indicated by the preliminary observations on Chinese White; and, for a fuller knowledge of the problem, it seems necessary to begin mounting the stigmas about two hours after pollination, and to discover more exactly at what stage the stigmas are in their most receptive state.

Table VIII shows the results obtained for the germination of pollen from (Iron × Rivet) F_1 on the stigmas of the F_1 itself, and on those of the parents. The number of grains that burst (classes (4) and (5) above) is given in each case.

In view of the inaccuracy that may have arisen from the stigmas not being fully receptive, it is not possible finally to decide what proportion of F_1 pollen is able to germinate; but this proportion is clearly a low one, and, pending fuller and more accurate investigations, certain tentative conclusions may be drawn.

A feature, which is of some interest if significant, is the variation in the number of burst grains. To make this clear the various proportions have been put down together in Table IX.

Grains burst through the presence of too much moisture. The results consistently indicate, therefore, that the Rivet and the F_1 stigmas are moister than the Iron stigmas. Correlated with this, we should expect

TABLE VIII.

F_1 *Pollen.*

(a) F_1 *stigmas. Pollinated* 27. vi. 24.

Hours after pollination	4¼	5	6½	7½	10¼	23
Tip protruded ...	0·07	0·07	0·04	0·03	0·05	0·04
Tube emerged ...	0·02	0·06	0·01	0·02	0·02	0·00
Empty	0·03	0·02	0·01	0·02	0·03	0·06
Not germinated ...	0·82	0·69	0·87	0·82	0·81	0·45
Burst	0·06	0·16	0·07	0·11	0·09	0·45
Total no. grains ...	146	116	209	197	115	78

(b) F_1 *Stigmas. Pollinated* 1. vii. 24.

Hours after pollination	4	5	6¼
Tip protruded ...	0·07	0·05	0·04
Tube emerged ...	0·04	0·08	0·02
Empty	0·06	0·03	0·06
Not germinated ...	0·55	0·62	0·67
Burst	0·28	0·22	0·21
Total no. grains ...	101	37	186

(c) *Rivet Stigmas. Pollinated* 5. vii. 24.

Hours after pollination	2¾	3¾	4¾	6¾
Tip protruded ...	0·05	0·03	0·05	0·09
Tube emerged ...	0·11	0·04	0·03	0·16
Empty	0·04	0·06	0·06	0·11
Not germinated ...	0·56	0·67	0·74	0·50
Burst	0·24	0·20	0·12	0·14
Total no. grains ...	133	203	165	164

(d) *Iron Stigmas. Pollinated* 1. vii. 24.

Hours after pollination	4	5	7*
Tip protruded ...	0·06	0·03	0·03
Tube emerged ...	0·01	0·00	0·01
Empty	0·02	0·04	0·05
Not germinated ...	0·86	0·90	0·87
Burst	0·05	0·03	0·04
Total no. grains ...	186	158	361

* Two or three well-developed tubes were present in the stigma, unattached to pollen grains. This suggests that the increase in the proportion of empty grains is significant.

Five stigmas of Iron, pollinated on 27. vi. 24, show very low germination; a stigma, pollinated 28. vi. 24, showed several well-developed pollen tubes, but germination was again low—it was too thickly pollinated for a count to be made.

TABLE IX.

Burst Grains.

Stigmas	Pollen		Proportions of burst grains
Iron	Rivet	(1)	0·05, 0·04, 0·04, 0·00
		(2)	0·03, 0·03, 0·04
	F_1		0·05, 0·03, 0·04
Rivet	Iron		0·11
	F_1		0·24, 0·20, 0·12, 0·14
F_1	F_1	(1)	0·06, 0·16, 0·07, 0·11, 0·09
		(2)	0·28, 0·20, 0·12, 0·14
	Rivet	(1)	0·05, 0·07, 0·04
		(2)	0·01, 0·09, 0·03
	Iron		Not counted, but clearly high

Rivet pollen to be adapted to moister conditions than Iron pollen; and, though the proportion of burst Iron grains on F_1 stigmas has not yet been counted, even a cursory examination of the slides leaves no doubt that this proportion is significantly greater than that of burst Rivet grains on the same stigmas.

On the stigmas of Iron and of the F_1, there is only one case in which the proportion of grains from which the tip of the pollen tube has protruded is not greater than the proportion in which the tube has emerged. This tends to confirm an impression, gained from examining the slides and from other sources, that many grains go no further than protruding the tip of the tube; and, indeed, this would not be surprising, for it is much easier, when trying to germinate wheat pollen artificially, to cause the tip of the tube to appear than to induce it to develop further.

With regard to the actual proportion of pollen that germinates, it is difficult, as we have already said, to reach a definite conclusion. However, the count given in Table VIII (*a*) should be fairly reliable, for the stigmas on which it is based were taken from the opposite side of the same ear as the stigmas supplying the data given in Table VII (*f*); and the latter showed a regular increase in germination, up to about 95 per cent. after 6 hours. Again, Tables VIII (*a*) and (*b*) do not differ widely, so we may reasonably accept the results given in the latter as well. Neglecting the result from Table VIII (*b*) 5 hours—in which only 37 grains were counted—the maximum value of the sum of the two proportions (tube emerged + empty) is 0·10 given by the stigma of Table VIII (*b*) mounted 4 hours after pollination. Allowing a proportion of 0·02 for the aborted grains, and assuming, in accordance with the indications of Table VII, that about 80 per cent. of the pollen that was able to germinate had done so by then, we may put the proportion of F_1 pollen that can germinate on F_1 stigmas at about 0·10. Similarly, on Rivet stigmas, it appears that germination may be as high as about 30 per cent. The stigmas of Iron show a much lower germination, but it hardly seems likely that out of nine of them none were fully receptive; granting this, we may deduce from Table VIII (*d*), 7 hours, that germination was about 5 per cent.

The lack of consistency in the results is puzzling. Much greater care was taken over the pollinations than is normally taken in crossing, and the preliminary observations on Chinese White did not indicate the existence of any such difficulty (a rough count on this variety gave: 4 hours = 0·04, 5 hours = 0·48, $6\frac{3}{4}$ hours = 0·76, 8 hours = 0·93, for the proportions of germinated grains). Perhaps the explanation is that the

results given in Tables VII and VIII refer to pollinations between widely different species or of the F_1 between them, and under such circumstances germination is less sure. The whole question must await more extended observation next season.

STERILITY.

Failure to set grain is one of the manifestations of sterility in wheat hybrids, and we have seen (p. 332) that this is, in most cases, caused by morphologically perfect egg-cells failing to become fertilised. The question whether these egg-cells are functional or not should be readily capable of answer by pollinating partially sterile ears with pollen from the parents of the original cross; and, as the F_1 plants only set grain, in 1923, in about 30 per cent. of the lowest two flowers of the spikelets, it appeared that such plants should provide a suitable test. Unfortunately, in the present season, the corresponding proportion of grains in F_1 ears is about 75 per cent., and this has rendered the work more difficult than was expected. The results of the various crossings are given in Table X. Care was taken, as far as possible, in selecting properly ripened pollen, and in seeing that the stigmas were receptive.

The mean proportion of grains obtained by pollinating the F_1 with pollen of the parents is 0·83. This actually exceeds the proportion of grains obtained from F_1 ears that were not bagged, by an amount equal to 2·6 times the standard error of the difference—despite the fact that it is most unlikely that perfect success in crossing was attained. Moreover, one of the F_1 ears pollinated by Rivet gave only a very low proportion of grains (Table X *a*), and it is probable that this was due to the

TABLE X *a*.

Results of pollinating (*Iron* ♀ × *Rivet* ♂) F_1.

Pollen	No. of flowers pollinated	No. of grains obtained	Proportion of grains
Iron	21	17	0·81
„	13	11	0·85
„	14	12	0·86
„	32	28	0·87
Rivet	30	26	0·87
„	22	18	0·82
„	15	7	0·47
Iron and Rivet together	25	24	0·96
F_1	33	17	0·52
„	20	13	0·65

F_1 × parents, mean proportion $=\frac{143}{172}=0{\cdot}83$

or, excluding 1 ear pollinated by Rivet, $\frac{136}{157}=0{\cdot}87$.

F_1 × self, mean proportion $=\frac{30}{53}=0{\cdot}57$.

TABLE X *b*.

Proportion of grains obtained from (Iron × Rivet) F_1, (1) from ears allowed to self naturally; (2) from ears enclosed in paper bags to prevent natural crossing; (3) from ears prepared as for crossing but without removing the stamens; that is, the spikelets from the top and bottom of the ear were removed, and also all but the first and second flowers of the remaining spikelets, but the latter flowers were untouched. In all cases only the first and second flowers of the spikelets were considered in arriving at these proportions.

	No. of flowers	No. of grains	Proportion of grains
(1)	1207	906	0·75
(2)	553	342	0·62
(3)	48	25	0·52

TABLE X *c*.

The results from crossing pure strains, and from the pollination of Rivet and Iron by the F_1, are here given. Of the former, only the most successful crosses have been selected, as it is possible that less care was taken with the crosses between pure lines than with the pollination of the F_1*.

♀	♂	No. of flowers	No. of grains	Propn. of grains	
Iron	Rivet	22	19	0·86	Mean propn. 0·90
,,	,,	21	20	0·95	
,,	,,	20	18	0·90	
Rivet	Yeoman	26	23	0·88	
,,	,,	20	18	0·90	
,,	Iron	19	17	0·89	
,,	,,	17	16	0·94	
Iron	F_1	10	2	0·20	Mean propn. 0·58
,,	,,	17	6	0·35	
,,	,,	18	16	0·89	
,,	,,	20	13	0·65	
Rivet	,,	20	10	0·50	
,,	,,	22	14	0·64	

* The mean proportion of success in all the crosses between pure strains was 0·79.

stigmas not being receptive; if we exclude this ear, the proportion of grains obtained by back crossing the F_1 rises to 0·87. Again, the proportion of successful pollinations between pure strains (Table X *c*) was 0·90; and if we suppose that technique was responsible for an equal number of failures in pollinating the F_1, the proportion of functional egg-cells in the latter would be put at $0{\cdot}83 \times 10/9 = 0{\cdot}92$. The former proportion, 0·87, exceeds 0·75 by 4·0 times the standard error of the difference; the latter, 0·92, exceeds it by 5·5 times. The possibility that these results might be explained by a variation in fertility up the length of the spike can be ruled out. It is true that in back crossing the F_1 only the spikelets from the central regions of the ear (about half the total number of spikelets) were pollinated, while the proportion of grains in ears that were allowed to self was obtained from complete spikes. But in F_1 ears (both bagged and unbagged) of the 1924 harvest there was no significant difference between the proportion of grains in the spikelets

in the central regions of the ear, and the proportion of grains obtained from complete ears.

It is concluded, first, that some functional egg-cells in the F_1 fail to become fertilised through lack of functional pollen; secondly, that morphologically perfect egg-cells—some of which were found (p. 332) not to be fertilised in partially sterile ears—are all, almost certainly, functional; finally, that the proportion of non-functional egg-cells is best arrived at by cytological examination, and that this proportion is certainly (p. 333) a low one.

The difference in proportion of grains, in ears that were bagged and those that were not, is remarkable. We shall see later that natural crossing occurs fairly frequently in partially sterile wheat hybrids, but I find it difficult to believe that this occurs sufficiently often to account for so large a difference. It seems more probable that bagging in some way affects the germination of pollen on the stigmas; for where so small a quantity of pollen is able to germinate, a comparatively slight change in external conditions may turn the scale from failure to success. The data at present available is insufficient, however, for us to give a definite answer to this question; or indeed, to know whether the fact that not all functional egg-cells are fertilised, in ears that were not bagged, arises from a variation in the quantity of functional pollen in different flowers, from the influence of external conditions on pollen germination, or from some other cause. Only one stigma from a flower that failed to set grain has been examined. It showed a number of well-developed pollen tubes, but these (see later, pp. 350–351) may have originated from foreign pollen that had fallen on the stigma shortly before mounting.

Before concluding this section, the results obtained by previous workers on sterility in wheat hybrids must be briefly reviewed. It is clear that Kihara's hypothesis (10)—that failure to set grain, failure of grains to germinate, and death of young plants, represent the elimination of all zygotes other than those formed when at least one gamete possessed either 14 or 21 chromosomes—is incorrect. Sax (11) supposes that gametes, whether male or female, which contain 17 or 18 chromosomes are unable to function; and in this way explains failure to set again, and the presence of aborted pollen; female fertility he measured by the average number of grains per spikelet. Sufficient evidence has been given to show that his theory, also, cannot be accepted.

As several investigators have measured sterility in wheat hybrids by the mean number of grains set per spikelet, it seems necessary to point out that this method is essentially unreliable. Whether or not a grain is

set in the third, fourth, fifth, or higher flowers of a spikelet depends more on the vigour of the tiller bearing the ear in question than on the amount of sterility: in small ears it is rare to find flowers above the third giving a grain, while in ears that are well developed even the sixth flower may sometimes do so. Mean number of grains per spikelet is therefore too much influenced by conditions other than amount of sterility to be a measure of this latter quantity. My own observations show that the most reliable simple method of measurement is the mean number of grains in the first and second flowers of all the spikelets in the ear; this quantity being independent of the vigour of the tiller, and, in general, sensibly constant for different tillers of the same plant: I have employed it throughout the present discussion.

It has been pointed out already that failure to set grain is subject to great seasonal fluctuation.

The Occurrence of Natural Cross Pollination in Wheat.

As already mentioned, natural crossing is very rare in wheat in this country; and it is therefore interesting to note that in partially sterile hybrids it occurs fairly frequently. It was first noticed in the F_3 of Rivet × Iron, harvested in 1922. In several cultures of this generation one or more plants that strongly resembled *T. polonicum* were found. It was thought at first that these were due to the accidental admixture of seed, but when their progeny were grown it was found that they were undoubtedly hybrids between *T. polonicum* and a Rivet-like plant. On examining the plan of the plots for 1921, it transpired that the Rivet × Iron F_2 had been grown next to a plot containing cultures from the cross *T. polonicum* × *T. durum*, var. *Kubanka*; this left little doubt that several of the plants from it had crossed naturally with plants from the latter plot. Further evidence was supplied when sorting the F_3: several cultures, the offspring of smooth chaffed plants, containing rough chaffed plants. That this was not the result of an error in classifying the F_2 plants was verified, as the latter had been kept; and in any case such an explanation could not apply to cultures containing 10 smooth to 3 rough chaffed plants, for rough and smooth differ by a single factor, and rough is dominant.

There is therefore no doubt that natural crossing takes place fairly frequently in these partially sterile hybrids. No record was made, unfortunately, of the number of cultures in which the offspring of natural crosses appeared; but as far as my memory serves, it could be traced in at least 15 out of 142 that should have been smooth chaffed. Doubtless

it had happened more often still, as no critical observations were made for characters other than rough and smooth.

In the light of the work that has been described, this phenomenon is readily understood. We have seen that many egg-cells fail to become fertilised through lack of sufficient functional pollen, and doubtless such egg-cells stand a strong chance of being fertilised by foreign pollen. Observation confirms this, for flowers containing ripe ovaries which have not been fertilised may remain open, with the stigmas protruding, for quite a long time in fine weather. It is interesting that although out-crossing had occurred in 1921, when the summer was hot and dry, yet examination, in 1923, of an F_3 from another *turgidum* × *vulgare* cross, failed to show its occurrence in a single one of some 140 or so F_2 plants; these were harvested in 1922, and in this year the weather was almost continuously cold and wet over the period during which most of the plants flowered. As the weather was favourable this year, 1924, during flowering, it is likely that out-crossing has taken place again.

From the foregoing conclusions it was expected that the phenomenon would prove not to be confined to partially sterile hybrids, but would be found in any plants showing some degree of failure to set grain; and this expectation has been borne out in the case of a dwarf variety of *T. vulgare* known as "Tom Thumb." This form set very little grain in the inclement summer of 1922, and in 1923 its descendants contained a number of new forms, which the 1924 results show to have originated from natural crosses.

These observations make it probable that the two cases of abnormal development, interpreted (pp. 332 and 333) as due to the late arrival of a pollen tube, arose from pollination, by foreign pollen, of ovaries that had so far not been fertilised owing to lack of functional pollen from the anthers of their own flowers. It has been pointed out, however, that other interpretations are possible.

T. dicoccum, var. *Ajar*, was partially sterile last year—grains being set in about 45 per cent. of the flowers. Whilst harvesting it this year, it was noticed that 4 plants, out of about 50, were probably F_1 between *Ajar* and a variety of *T. turgidum* that was grown next to it last year. This indicates, therefore, that about 7 per cent. of the ovaries of *Ajar* that failed to become selfed were cross pollinated. This is a high proportion, but to explain in this way the difference in the proportion of grains obtained from bagged and unbagged ears of Iron × Rivet F_1 (see p. 348), we should have to assume that about 35 per cent. of ovaries that were not selfed were cross pollinated.

Summary and Conclusions.

The reduction divisions follow the same course in both megaspore and microspore mother cells, and chromosomes are lost with approximately equal frequency in the two cases. But the chance that a univalent chromosome will be included within the nucleus of the innermost megaspore is probably somewhat less than the chance of its inclusion within a microspore nucleus. A small proportion of ovules from F_2 and F_3 plants are found to be empty at the time the ear begins to flower; but, with these exceptions, the development of the embryo-sac from the megaspore is normal, and only functional egg-cells are obtained. Many of the latter, however, fail to become fertilised through lack of sufficient functional pollen; and in consequence natural crossing may sometimes take place. Embryo and endosperm development are normal. A considerable number of grains from partially sterile plants do not germinate, or give plants that do not survive; but these contingencies do not occur often enough to account for the absence of the chromosome combinations that are not found—so long as we assume that the frequency of the various classes of functional male gametes is the same as that of the microspore classes. A method of studying the germination of pollen grains on the stigma has been given. Most of the morphologically perfect pollen grains, from F_1 plants, do not germinate on the stigmas of the F_1 or on those of either parent.

It is concluded that the failure of microspores to give pollen grains that germinate is selective with respect to the number of chromosomes they contain—failure being least likely with those that possess either 14 or 21 chromosomes.

It is possible, on the one hand, that only male gametes with 14 or 21 chromosomes effect fertilisation; on the other, that the elimination of gametes with an intermediate number of chromosomes is only partial—some of the expected chromosome combinations, that are not found in the zygotes, being formed, but later eliminated in their turn, or surviving only sufficiently often to escape notice.

The number of pollen grains that germinate on the stigma is influenced by the degree of receptiveness of the latter, and for this reason the results obtained for the germination of F_1 pollen are only provisional. They indicate a much higher proportion, about 0·30, on the stigmas of the *turgidum* parent than on those of the F_1, where the proportion is about 0·10, or on those of the *vulgare* parent, where it is probably about 0·05. They suggest, also, that Rivet and F_1 stigmas are moister than those of Iron (*vulgare*).

Furthermore, that many F_1 pollen grains are unable to do more than protrude the tip of the pollen tube.

The main outlines of the cytology of these crosses are therefore becoming fairly clear, but confirmation is desirable before definite conclusions are reached. Two facts, which are already striking, do fit in with the theory: the rapidity with which the chromosome number 28 is regained, and the comparative slowness of attaining the number 42. In plant A (1), with 31 chromosomes, if we assume the chance of inclusion of a univalent in the nucleus of the innermost megaspore to be 0·12, and that only male gametes with 14 chromosomes function, nearly 70 per cent. of its offspring have 28 chromosomes. In plant B, with 38 chromosomes, the chance of inclusion of a univalent is 0·29, and assuming that only male gametes with 21 chromosomes function, less than 10 per cent. of its offspring would have more than 40 chromosomes. These results are roughly in accord with observation.

A state of affairs similar, in some respects, to that outlined above, is found in *Oe. lata*, and in *Datura* mutants with an extra chromosome. The absence of 16 chromosome plants among the progeny of *Oe. lata* is well known, and Lutz (13) believes that female gametes containing either 7 or 8 chromosomes function, but only male gametes with 7 chromosomes. In the Globe mutant of *Datura* the extra chromosome is transmitted by about 30 per cent. of the ovules, but only about 3 per cent. of the pollen grains (15), and Buchholz and Blakeslee (14) give evidence that this is the result of a slower growth of tubes from pollen grains containing the extra chromosome. They also suggest that there may be a greater mortality of Globe zygotes during embryonic development. Here, again, progeny with two extra chromosomes are not found. The mutant Enlarged in *Nicotiana*, recently described by Clausen and Goodspeed (16), behaves very similarly to the Globe mutant in *Datura*, but gives a small number of Super Enlarged plants, which, presumably, contain two extra chromosomes. It appears, therefore, to be general that the possession of an abnormal number of chromosomes should interfere with the normal development of a microspore, or the germination of a pollen grain; though it is questionable how far the state of affairs in wheat hybrids is comparable with that found in *Oenothera*, *Datura*, or *Nicotiana*, as in the latter three cases the extra chromosome is probably identical with one of those normally present in the gametes, and in wheat this may not be so.

Reduction in the wheat hybrids is carried out with greater regularity than is usually the case with hybrids between species with different

numbers of chromosomes. This is shown in the general character of both divisions; by the fact that in every case yet observed four microspores are formed—though the separation of a univalent, with a small quantity of cytoplasm, to form a minute fifth cell occurs as a great rarity; and finally, by the evidence which is accumulating to show the regularity with which chromosomes are lost. Associated with this we find almost complete egg-cell fertility; and it would be interesting to know how far, in other genera, a correlation between amount of fertility and regularity in reduction exists. The evidence available is limited, but Jesenko's observations on the wheat × rye hybrid (17), and the results obtained from various *Papaver* crosses (18, 19) do suggest on the whole that the greater the irregularity at reduction the greater the sterility. Other instances might be cited, but none of these examples have been worked out with sufficient precision to make adequate generalisation possible; and in any case, if the deciding factor in the degree of sterility is the constitution of the microspores and megaspores that are formed, factors other than the amount of irregularity at reduction will influence the result—though this may be the most important one.

On general grounds, it is natural to assume that the fact that some of the chromosomes from different species are able to form bivalents shows an essential similarity between them. The extent of this similarity can only be discovered by an accurate knowledge of the reduction divisions, amount of sterility, and genetic behaviour of the hybrid; and in this connection the results of Goodspeed and Clausen (20) on crosses between *N. tabacum*, $x = 24$, and *N. sylvestris*, $x = 12$, are of interest. Based on these results, and believing that both species had the same number of chromosomes, they formulated the "reaction-system hypothesis." By growing the F_1 under reduced conditions, and pollinating from either parent, a few seeds are obtained—not more than 1 per cent. of the number ordinarily produced. With *sylvestris* pollen, about 10 per cent. of the plants obtained closely approximate to this species, and the remainder are abnormal in type; with *tabacum* pollen, all the plants approximate to *N. tabacum*, though showing considerable variation. In a later paper, Goodspeed (21) suggests that the functional egg-cells of the F_1 contain either the 12 *sylvestris* or the 24 *tabacum* chromosomes; but finds a difficulty in assuming that the 12 of the former ever pass all to the same pole, and even greater difficulty with the 24 of the latter species. Though the corresponding wheat hybrids have not yet been analysed exactly, the results suggest that plants with more than 35 chromosomes are always distinctly of the *vulgare* type: indeed the F_1 resembles *vulgare*

rather than *turgidum*; and a plant with 37 chromosomes, typically *vulgare* in everything except its sterility, has been found. In addition, we have plants with 28 chromosomes that include a wide range of *turgidum* forms, and perhaps some abnormal types; and plants, with a chromosome number intermediate between 28 and 35, that are mostly abnormal in type and difficult to classify. This suggests that only a single set of the extra 7 *vulgare* chromosomes are necessary to give a *vulgare*-like plant—the addition of a second set of 7 making very little difference. The observations are not sufficiently extended to justify more than a working hypothesis, but if we give them a provisional acceptance the *Nicotiana* results are easier to understand. *Tabacum* pollen would give plants that varied in chromosome number from 36 to 48—assuming, with Goodspeed, that the F_1 forms 12 bivalents—and these would resemble the *tabacum* parent by reason of the 12 extra *tabacum* chromosomes introduced by the male gamete. *Sylvestris* pollen would give some plants with 24 chromosomes, *sylvestris* in type; and others, with from 24 to 36 chromosomes, that are mostly abnormal. With regard to the relationship between the 12 *sylvestris* chromosomes and the 12 from *tabacum* with which they pair, it is difficult, as Goodspeed points out, to assume that all of the former pass to one pole. Much simpler is it to regard the two sets as being very similar to one another. On this view, the extent of the variation of the plants obtained from back-crossing the F_1 with *sylvestris* should show the extent to which the two sets of 12 chromosomes differ; though, here again, some combinations may have been eliminated by the abortion of the megaspores containing them. In the wheat example, it may be possible for us to carry out a sufficiently exact analysis for us to solve this problem.

Just as this paper was going to the press, a recent paper by Kihara (25) came into my hands. It is not possible at the present time to consider his results fully; but some of his conclusions are at variance with mine, and these I have considered shortly in the Appendix.

APPENDIX.

In a recent paper, Kihara (25) has brought forward a mass of fresh facts that are of great interest and importance for the solution of the problem we are considering. Some of his results offer a striking confirmation of the conclusions I have reached in the present paper. These results, and those of his conclusions which differ essentially from my own, I propose to consider here.

First, I must mention that plants containing what I have in my former

paper (1) called non-viable chromosome combinations have appeared occasionally in his cultures—*e.g.* a plant with 40 chromosomes that form 20 bivalents at reduction. These plants only appear occasionally, they are usually of dwarf habit, they set very few grains, and of the grains they do produce very few germinate. They do not appear often enough to affect in any essential manner the conclusions already reached, and I shall not, here, consider them further. They are referred to by Kihara as plants with "sterilen Kombination," or shortly as st. K. plants.

Kihara has found experimentally the frequency with which the various possible chromosome numbers are found in the descendants of plants with 38, 39, 40, and 41 chromosomes. For the sake of simplicity, we will consider here the results for the 41 chromosome plants, for which, also, the data is most extensive. From observations on the frequency of lost chromosomes in the microspores, he arrives at the frequency of gametes, male or female, with 20 and 21 chromosomes respectively, assuming that all microspores and megaspores give functional gametes. The further assumption of random mating gives the frequency of zygotes with 40, 41, and 42 chromosomes. The ratio of 41/42 chromosome zygotes so found agrees with the experimental results; and this is the case, also, with the offspring of plants with 38 and 39 chromosomes. He concludes, therefore, that random mating between gametes of the same class frequencies does take place; and that in the case of the 41 chromosome plant for example, the 40 chromosome zygotes represent failure to set grain, failure of grains to germinate, etc., and the occurrence of st. K. plants; hence, that in these hybrids sterility is "zygotische" and not "gametische." This final conclusion is largely at variance with my own. He supports his conclusion by the fact that "Durch die direkte mikroskopische Beobachtung des Plasmareichtums und der starken Turgeszenz im Wasser kann die Lebensfähigkeit der meisten Pollenkörner der pentaploiden Bastarde auch bestätigt werden. Die Sterilität dieser Bastarde kann daher nicht der Unfähigkeit der Pollenkörner selbst zugeschrieben werden, ..." The evidence offered by my pollen germination tests, and the results from back-crossing the F_1, are sufficient to show that these statements are not correct.

Grain germination tests were carried out, but no definite conclusion was reached. With regard to failure to set grain, however, he finds that the average number of grains per ear for plants with 36, 37, ... 42 chromosomes increases with the increase in chromosome number, as would be expected if failure to set grain is due to the early death of zygotes containing the non-viable chromosome combinations (the

numerical calculations need not be considered here). I have pointed out that number of grains per spikelet is unreliable as a measure of failure to set grain, and the objections to this measure apply still more forcibly to the quantity average number of grains per ear; in fact Kihara's results do suggest that the standard deviation of the mean number of grains per ear is sufficiently great to render his conclusions concerning change in fertility uncertain. In any case, it is clear from the evidence that I have brought forward that failure to set grain is not due, except perhaps in rare cases, to the early death of zygotes; but is caused, at any rate as a general rule, by the fact that fertilisation often fails from lack of sufficient functional pollen.

It is therefore clear that Kihara's view—that random mating between gametes of the same class frequency occurs, and that sterility is zygotic and not gametic—is not consistent with much of the evidence that I have brought forward in the present paper. In an appendix to his paper he gives results that strongly support my own conclusions. Reciprocal crosses between a 41 chromosome plant and a pure strain of wheat with 42 chromosomes gave the following results:

(a) 41 *chromosome* ♀ × 42 *chromosome* ♂ *gave:*

No. of chr. in zygote	41	42
Frequency	11	4

(b) 42 *chromosome* ♀ × 41 *chromosome* ♂ *gave:*

No. of chr. in zygote	41	42
Frequency	6	8

From (*a*) we can conclude that the chance that a univalent chromosome was included in the nucleus of the innermost megaspore was $4/15 = 0{\cdot}26$[1]. This agrees closely with the chance that I found (p. 326) for the inclusion of a univalent in the nucleus of the innermost megaspore of a plant with 38 chromosomes (in the plant with 31 chromosomes the corresponding chance was 0·12; there is other evidence that in plants with less than 35 chromosomes the frequency of chromosome loss is greater than in plants with more than 35 chromosomes). From (*b*) we see that the chances that fertilisation is effected by gametes with 20 and 21 chromosomes are 0·43 and 0·57 respectively. From (*a*) and (*b*) the frequencies of the zygotes would be:

No. of chr. in zygote	40	41	42
Frequency	0·32	0·54	0·14

For the 41 and 42 chromosome zygotes from a 41 chromosome plant Kihara has found the relative frequencies 59 : 18. The two results are

[1] The only assumption here made is that the pollinations were as successful in the case of the 20 chromosome egg-cells as with the 21 chromosome egg-cells.

therefore in close agreement; and from the results of my grain germination tests, a proportion of 0·32 for grains that do not germinate, plants that do not complete development, and perhaps one or two of the st. K. plants found by Kihara, does not seem too high.

Turning now to the comparative frequencies of (1) microspores with 20 and 21 chromosomes, and (2) the number of gametes, with 20 and 21 chromosomes respectively, that effect fertilisation; we find for (1) the values 0·74 and 0·26[1], and for (2) 0·43 and 0·57. This means that the chance that a 21 chromosome microspore will give a gamete that effects fertilisation is to the corresponding chance for a 20 chromosome microspore as 100 : 43. The difference may be due partly to the 20 chromosome microspores being more likely to give an obviously sterile pollen grain or one that does not germinate, and partly perhaps to such pollen grains giving tubes that travel more slowly. It does not seem unlikely that a microspore with 19 chromosomes would have a still lower chance of giving a male gamete that functions, say perhaps about 0·15; and so on for microspores with the other possible chromosome numbers. It would be interesting to know what class of microspores have the lowest chance of giving a male gamete that functions; but this question we must leave for further work.

The evidence clearly gives strong support to the conclusion I had already reached: "that the failure of microspores to give pollen grains that germinate (more accurately, male gametes that effect fertilisation) is selective with respect to the number of chromosomes they contain —failure being least likely with those that possess either 14 or 21 chromosomes." There also seems little doubt that the grains from which mature plants are not obtained do represent the non-viable chromosome combinations.

I am indebted to my wife for much assistance rendered during the course of this investigation.

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[1] Assuming the same frequencies as for the megaspores. I have already shown that the two are probably not quite the same (p. 326), but the difference would not be great enough to affect the conclusions in any essential manner.

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All figures were drawn with the aid of a camera lucida.

Figs. 1–6. Reduction in the Megaspore Mother Cell. × 1000.

Figs. 1–2. Heterotype metaphase.

Fig. 3. Heterotype anaphase. The descendants of the bivalents have reached the poles. The univalents have split, and the halves are shown joined by dotted lines; the other halves of the two chromosomes marked *x* have either reached the pole, or were disturbed by the razor, part of the cell being present in the next section.

Fig. 4. Interkinesis.

Fig. 5. Homotype, metaphase and anaphase.

Fig. 6. Completion of the divisions. Part of the two outer cells, marked *a*, were cut off, and are in the next section.

Fig. 7. Two adjacent sections. The outermost cells are degenerating. The innermost cell was cut, and the two portions are marked *a*.

Fig. 8. The three outer cells are degenerating (*deg.*). The third cell was cut, and is present in the two adjacent sections.

Fig. 9. The three outer cells have degenerated, and the innermost megaspore has begun to enlarge.

Figs. 10–13. Development of the Embryo-sac.

Figs. 10–12, and 13 *b–d*, × 520; Fig. 13 *a*, × 230.

Fig. 12 *a*. Embryo-sac.

Fig. 12 *b*. Synergids from adjacent section. *g* = staining globule.

Fig. 13 *a*. Embryo-sac.

Figs. 13 *b*, *c*, and *d*. Egg-cell and one synergid, polar nuclei, and antipodal, from embryo-sac shown in *a*.

Figs. 14–17. Stages in Fertilisation. × 520.

Fig. 14 *a*. Fertilised egg-cell, and synergid that was attacked by pollen tube.

Figs. 14 *b* and *c*. From same section as 14 *a*. Incompletely differentiated antipodal, and endosperm nucleus.

Fig. 15 *a*. Egg-cell and male gamete.

Fig. 15 *b*. Synergid, after attack by pollen tube, showing darkly staining fragments, and granules. Part of the second synergid, and of the egg-cell shown in 15 *a*, are present in this section; their positions are indicated by dotted lines.

Fig. 15 *c*. Polar nuclei; male gamete entering.

Fig. 16 *a*. Egg-cell, and male gamete within its nucleus.

Fig. 16 *b*. Synergids; the one that was attacked containing densely staining mass.

Fig. 16 *c*. Polar nuclei; male gamete entering.

Fig. 17. First division of fertilised egg-cell; attacked synergid.

Figs. 18–21. Abnormalities.

Fig. 18. Micropylar end of embryo-sac, with degenerating egg-cell, etc., × 520.

Fig. 19. Part of embryo-sac, with degenerating embryo and endosperm. × 105.

Fig. 20 *a*. Normal, many-celled, embryo; attacked synergid. × 235.

Fig. 20 *b*. Degenerating polar nuclei, from same embryo-sac. × 520.

Fig. 21. Part of ovule; containing degenerated embryo and endosperm. × 55.

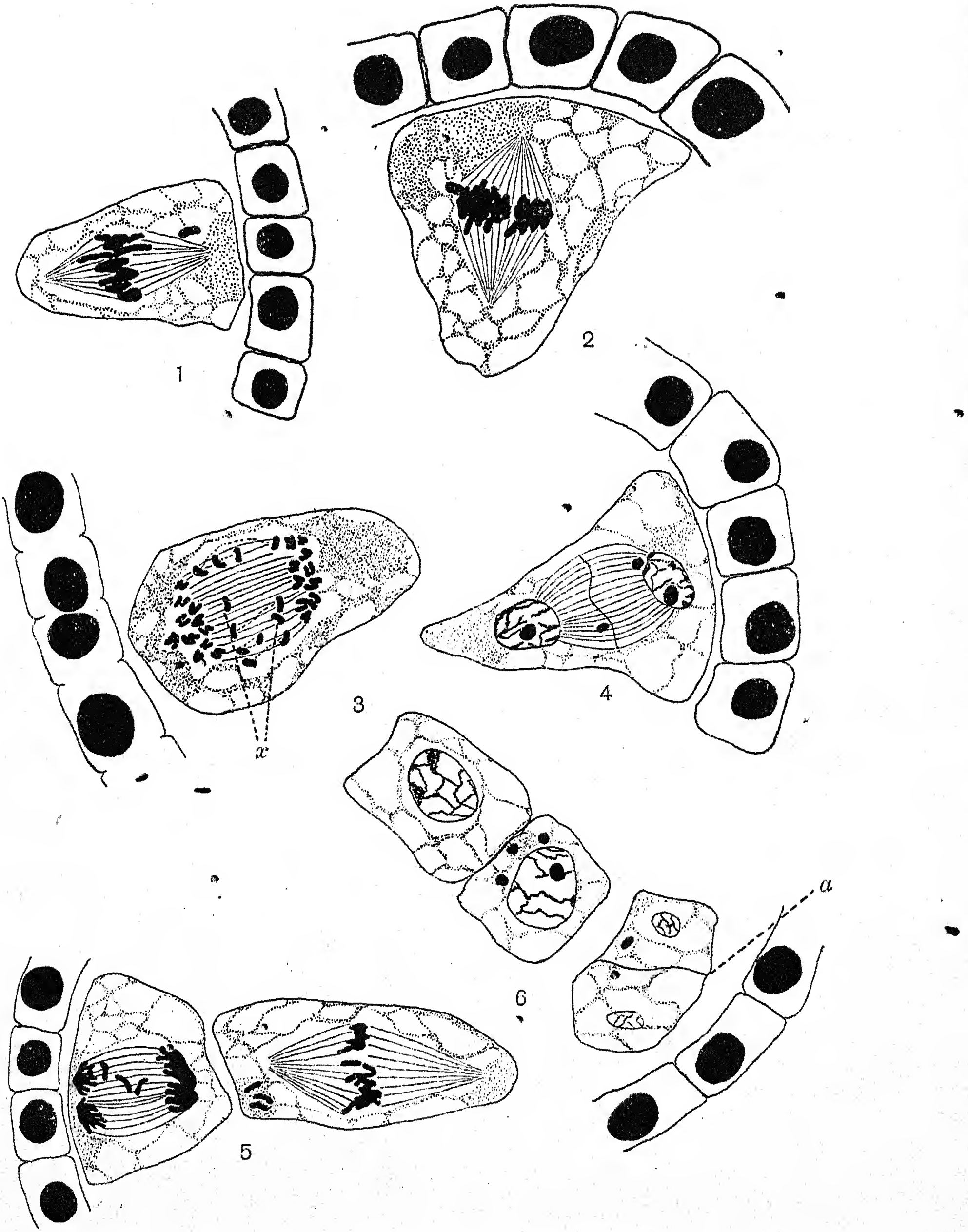
anti = antipodal, *e.c.* = egg-cell, *end* = endosperm nucleus, *p.t.* = pollen tube, *syn* = synergid.

Figs. 22–27. Germinating Pollen Grains.

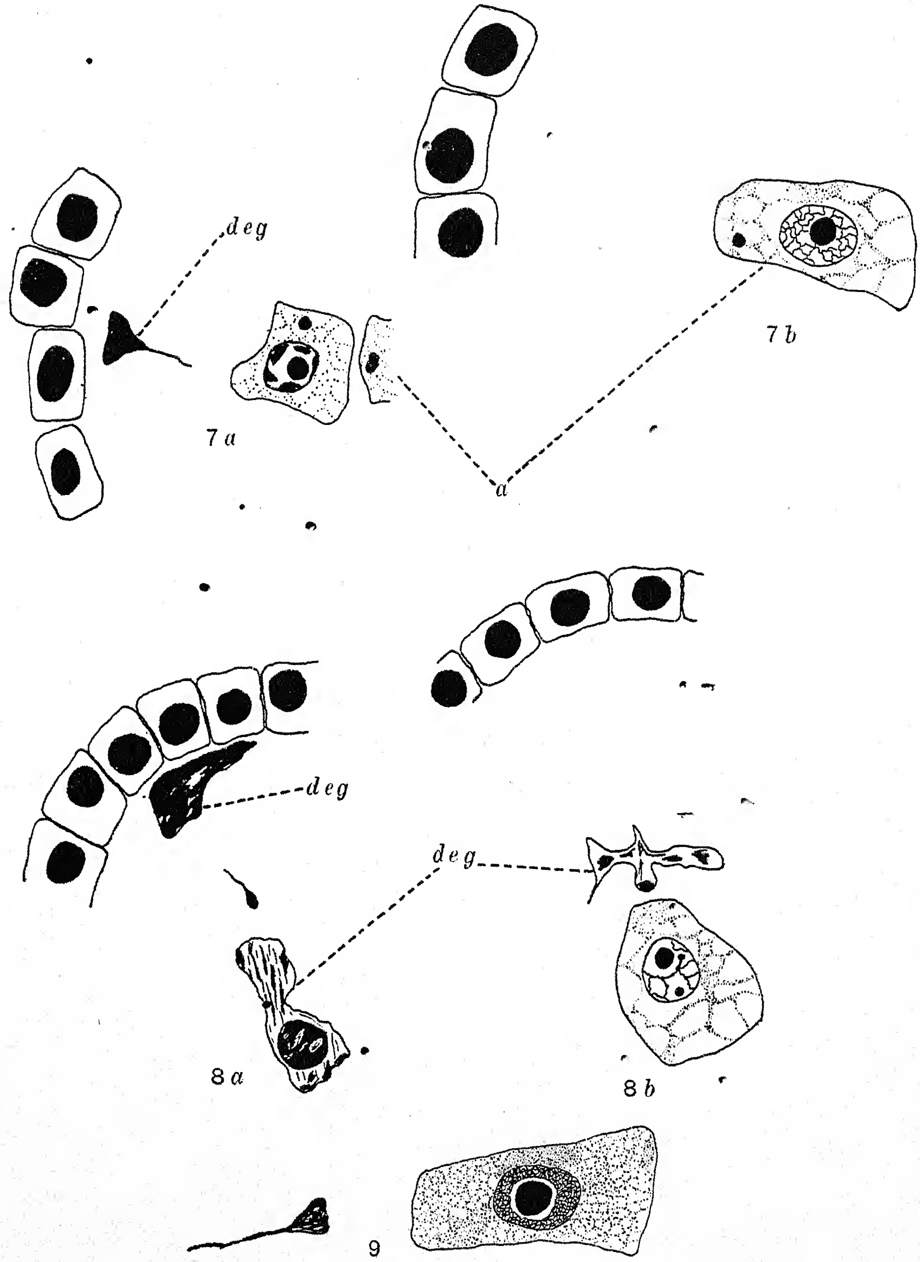
Figs. 22–25. *T. vulgare*, var. Chinese White. × 405.

Fig. 26. Iron ♂ on (Iron × Rivet) F_1 ♀. × 455.

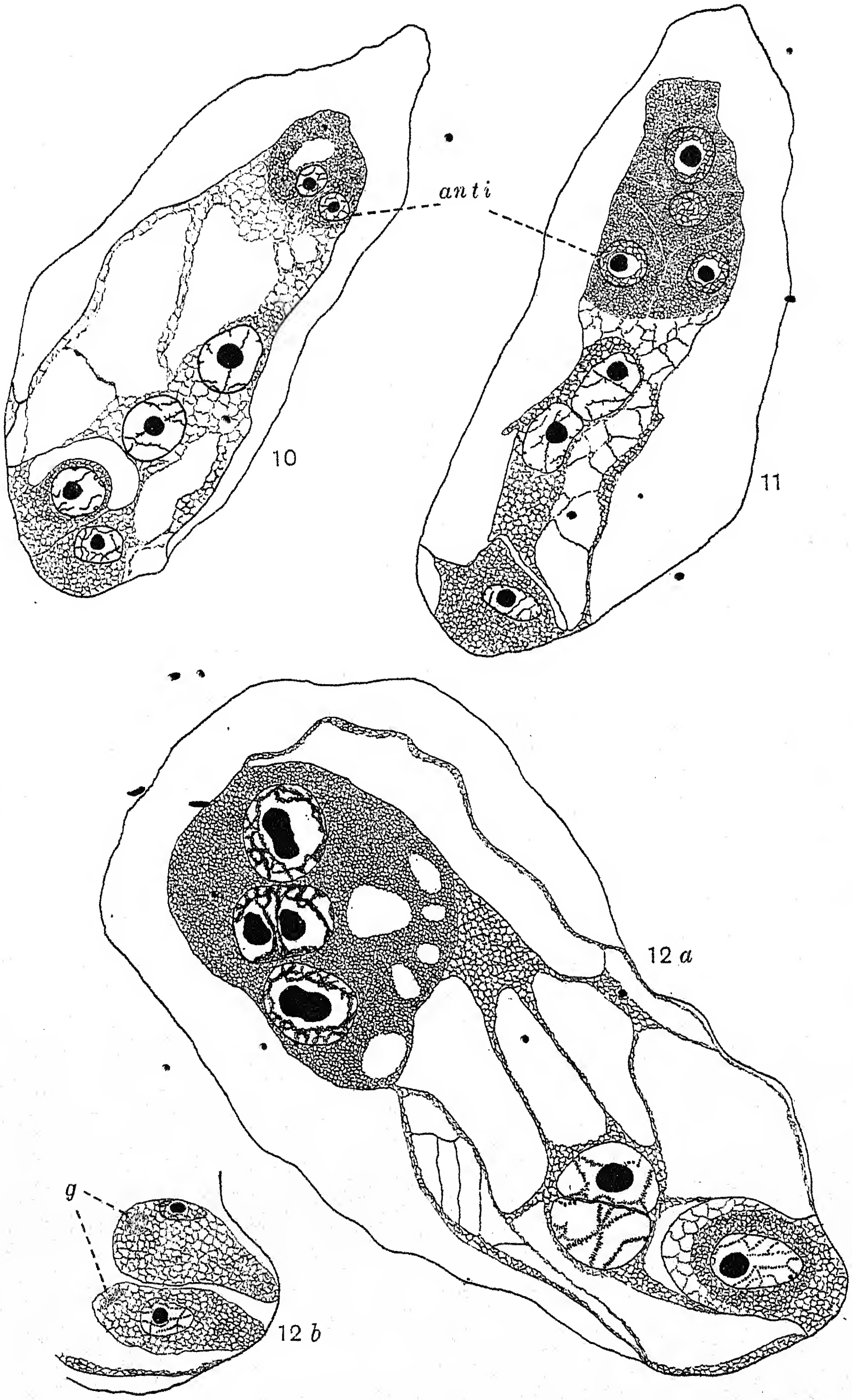
Fig. 27. Iron ♂ on (Iron × Rivet) F_1 ♀. × 220.



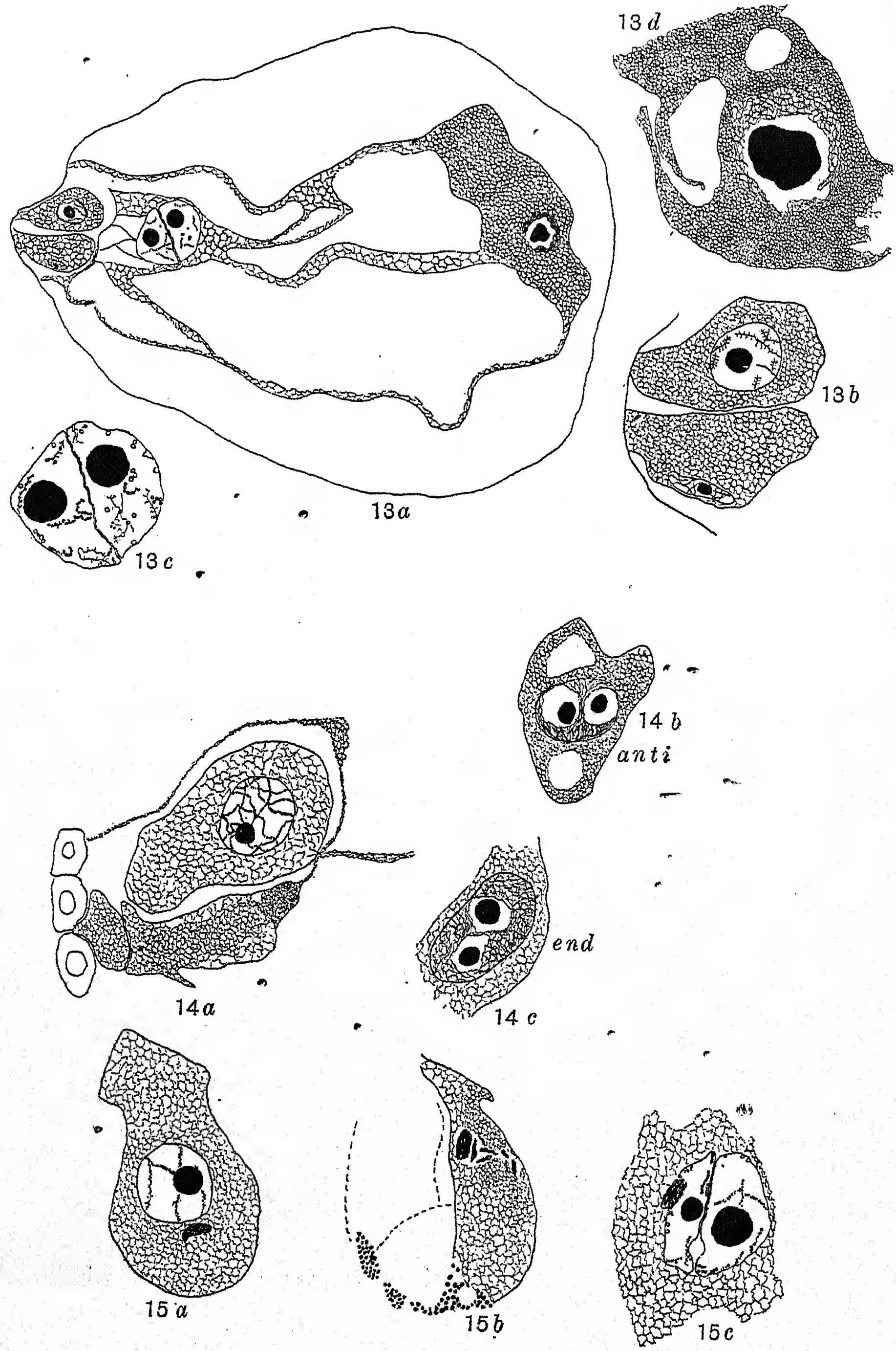
Figs. 1–6.



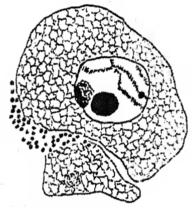
Figs. 7–9.



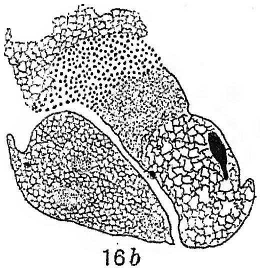
Figs. 10–12.



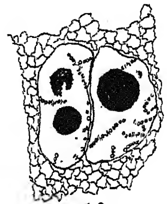
Figs. 13–15.



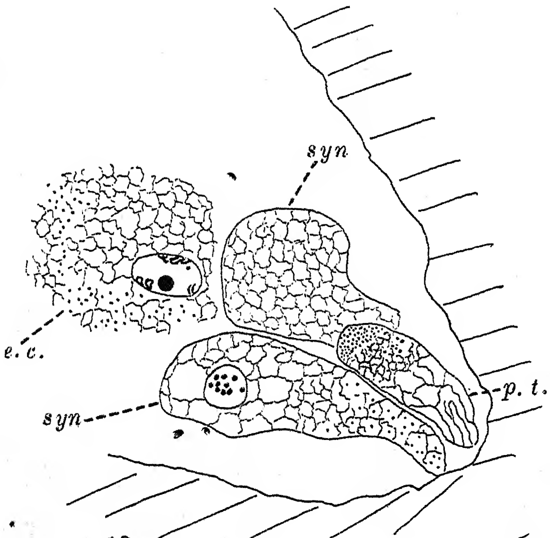
16 *a*



16 *b*



16 *c*



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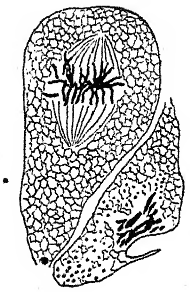

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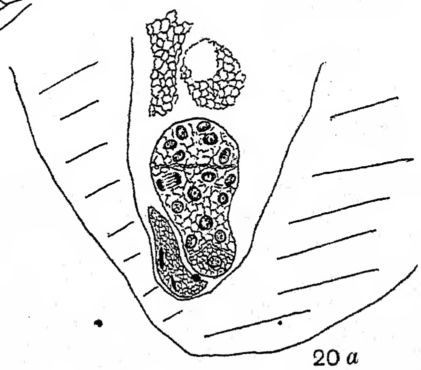
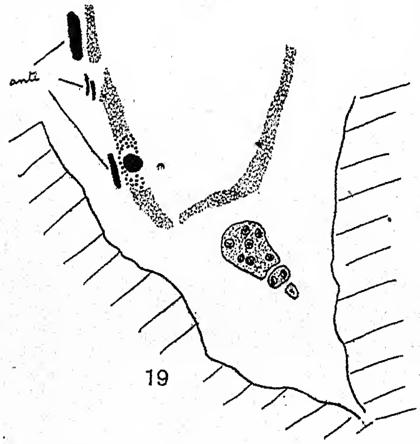


20 *a*



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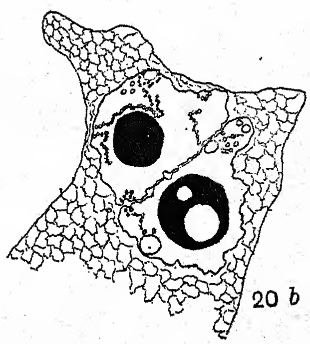
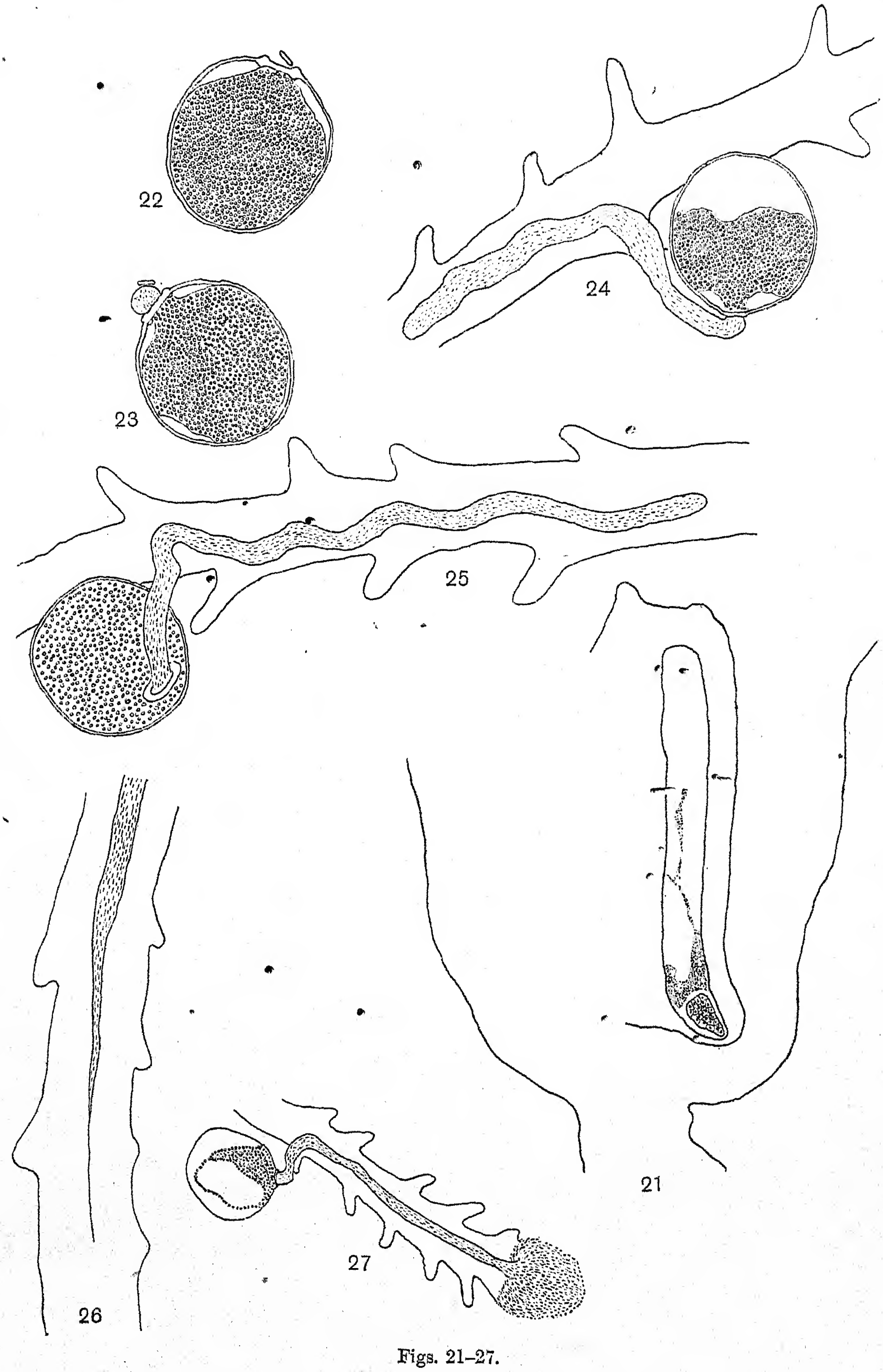


20 *b*

Figs. 16–20.



Figs. 21–27.

THE INHERITANCE OF HORNS IN THE GOAT.

By S. A. ASDELL,
Animal Nutrition Institute, School of Agriculture, Cambridge University
AND F. A. E. CREW,
Animal Breeding Research Department, The University, Edinburgh.

Introduction.

The earliest reference in scientific literature to this subject seems to be that of Bateson and Saunders (1902) who suggested that "the fact that the hornless breeds of goats still give some horned offspring is probably referable to the same cause (heterozygosity). The point is, of course, not certain, but from the analogy of cattle we may anticipate that the hornless form is dominant." However, when an analysis of the Herd Book of the British Goat Society was made by Davies (1912), it was found that among the 2500 entries there were 32 instances of two horned parents yielding a hornless kid. These cases, of course, cannot be accommodated by the suggestion that the polled condition, in its relation to the horned, is one of simple dominance. In this paper the analysis of the Herd Book is brought up to date in a further endeavour to disclose the genetic relationship of these two characters.

The Data.

The Herd Book of the British Goat Society during the years 1886–1924 (September) gives certain particulars of the characterisations of 9064 goats grouped in the following classes: general sections 6776; Anglo-Nubian 1650; Swiss or Saanen 61; Toggenburg 573 and Nubian 4, and against the name of a goat there is entered the detail Horned (*H*), Hornless (*P*), Disbudded (*D*), or, in a few cases, Scurs (or slugs). Since it is with these entries that this analysis is concerned it is necessary in the beginning to enquire as to their validity.

On examination it soon became manifest that many entries failed to distinguish between the natural and the artificial hornless individual. Both the polled and the disbudded are hornless, but whilst a few breeders regard the disbudded as horned the majority refer to them as polled. Since 1915, however, the Society has demanded that all disbudded

TABLE I.

	$H \times H = H$	$H \times D = H$	$D \times D = H$	$H \times H = D$	$H \times D = D$	$D \times D = D$	$H \times H = P$	$H \times D = P$	$D \times D = P$	Total	Remarks
1–1000	62	0	0	0	0	0	6	0	0	68	—
1885–1901: 1000	91·2 %	—	—	—	—	—	8·8 %	—	—	6·8 % of all	—
1001–2000	64	3	0	26	0	0	35	1	0	129	$3H \times H = P$ known to be wrong
Toggenburg 1–275; Anglo-Nubian 1–600 (500 are duplicated and are neglected)											
1901–1911: 1375	50·0 %	2·3 %	—	20·2 %	—	—	27·1 %	0·8 %	—	9·4 % of all	—
2001–3000	39	20	4	3	0	0	4	6	0	76	$3H \times H = P$ $4H \times D = P$ known to be wrong
Toggenburg 276–390; Anglo-Nubian 601–1000; Swiss or Saanen 1–9											
1911–1919: 1624	51·5 %	26·3 %	5·3 %	4·0 %	—	—	5·3 %	8·0 %	—	4·7 % of all	—
3001–4000	63	14	0	4	2	0	6	1	2	92	$4H \times H = P$ known to be wrong
Toggenburg 391–440; Anglo-Nubian 1001–1242											
1919–1920: 1292	68·5 %	16·3 %	—	4·4 %	2·2 %	—	3·3 %	1·1 %	2·2 %	7·1 % of all	—
4001–5000	30	11	1	2	3	3	0	1	2	53	—
Toggenburg 441–477; Anglo-Nubian 1243–1375											
1920–1922: 1169	56·8 %	20·8 %	2·0 %	4·0 %	6·0 %	6·0 %	—	2·0 %	4·0 %	4·5 % of all	—
5001–6000	24	8	2	3	4	3	1	5	3	53	$1H \times H = P$ known to be wrong
Toggenburg 478–540; Anglo-Nubian 1376–1570; Swiss or Saanen 10–48											
1922–1923: 1295	45·3 %	15·1 %	4·0 %	6·0 %	8·0 %	6·0 %	2·0 %	9·0 %	6·0 %	4·1 % of all	—
6001–6776	12	6	0	3	4	6	0	0	2	33	—
Toggenburg 541–573; Anglo-Nubian 1571–1650; Swiss or Saanen 49–61											
1923–1924: 900	36·4 %	18·2 %	—	9·1 %	12·1 %	18·2 %	—	—	6·0 %	3·7 % of all	—
Total $H \times H$ type of mating 504	294	62	7	41	13	12	52	14	9	504	

individuals shall be entered as such. Another source of error has its origin in the fact that not every kid is entered in the Herd Book. It is the practice to slaughter the unwanted male kid, and this applies particularly to the horned male. Further, it was found on enquiry that several of the entries were definitely and wholly inaccurate. This was considered justification for questioning the validity of any breeding result that was exceptional.

Evidence as to whether or not the polled condition is a simple dominant to the horned is most easily obtained from an examination of the matings of two horned individuals. If it can be shown that such a mating can undoubtedly yield hornless offspring it must follow that the suggestion put forward by Bateson and Saunders is incorrect.

Among the progeny of 504 matings of Horned × Horned (including Horned × Disbudded and Disbudded × Disbudded) recorded, 75 kids are entered as hornless. It should be stated that for purposes of discussion the female is regarded as being monotocous, and that one and the same mating is therefore often counted twice or thrice. The figures as they stand furnish conclusive evidence against the contention of Bateson and Saunders that the hornless condition is a simple dominant. But in view of the three causes for error mentioned above, each of which is quite common, it is reasonable to assert that if the slightest doubt attaches itself to any of these cases in which it is recorded that a horned, by horned mating, has yielded a polled kid, that case can be ignored.

It has been impossible to examine in a critical fashion all of these cases, but certain of them were so examined, and it was found (1) that some of the hornless offspring of two horned parents, when themselves bred, behaved as horned individuals, the horned condition being a recessive. It is reasonable to suggest that these individuals entered as hornless were really disbudded; (2) that certain pedigree charts showed an apparently haphazard sporadic recurrence of the hornless condition. It is reasonable to assume that these entries were fallacious since the hereditary mechanism, as far as is known, does not lead to such results; and (3) that since 1915 the entries of a polled kid out of horned parents almost disappear and in their place are to be found $H \times D = P$, or $D \times D = P$. Here another source of error became manifest. It is often impossible to distinguish between a kid that when adult is to possess horns from one that will exhibit scurs. This being so, in disbudding such a kid the breeder, or more probably the herdsman, may be operating on either sort and the entry will record his impression and not necessarily the genetic constitution of the kid. In view of this, further particulars

concerning certain entries were sought and obtained and it was found that two females, 1344 and 1345, and one male, 2611, registered as horned were actually polled, that one male, 1907, registered as horned was actually an individual with scurs, that one polled male, 3326, and two polled females, 3325 and 3333, were in reality horned, and that in one case in which a horned dam, 1084, was recorded she was not the mother at all, the actual mother being a polled individual, 1018. In one case only, 3895 ♂ *P* Sherwood Archer ex 2105 ♀ Stanmore Bluebell by 3175 ♂ Sepa, was it still maintained by the breeder that the particulars as recorded were correct. This experience finally fixed the impression that all entries of exceptional hornless individuals were possibly, if not probably, erroneous, for if in 14 out of 15 cases available for thorough examination error could so readily be demonstrated it became reasonable to assume that similar errors would be as frequent, if not more so, in cases further back in the Herd Book.

In addition to these 15 cases concerning which reliable information was still obtainable, 60 other cases of hornless kids out of horned parents are recorded. It was found that many of these were not used for breeding, and that there was reason to hold that the records of those that were used were incorrectly given. The record of 1365 ♂ *H* Sedgemere Principio can serve as an example. Part of it is as follows:

Hornless offspring	Horned dam
1427 ♀ Sedgemere Aldina Not bred	T136*H* Sedgemere Almina. Also bred 2*P*
1647 ♀ Copthorne Mango Bred 4*P* by *P*	T351*H* Trima. Also bred 1*H*
1810 ♀ Copthorne Lemon Bred 4*H*, 2*D*, 6*P*	T229*H* March. Also bred 2*P*
1811 ♀ Copthorne Sultana Bred 2*D*, 6*P*	T229*H* March. Also bred 2*P*
1873 ♀ Hazlemere Topsy Bred 1*H*	1835*H* Dolly Grey. Also bred 1*P*

It is to be noted that S. Principio was used in a herd where most of the horned individuals were disbudded and entered as hornless. It is also to be noted that information ascertained from the breeder shows that this goat was disbudded as a kid. The operation was effective on one side, but on the other the horn continued to grow but was periodically knocked off by the goat. He was entered as Horned. His sire, T97, Sedgemere Paris, imported, was hornless and bred 11*P*, and 2*H* including S. Principio. His dam, Sedgemere Faith, imported was also hornless, and produced a number of kids, the only horned one being S. Principio. Much importance cannot be attached to his breeding record, as disbudding affects the accuracy of the Herd Book at this period. When bred with

horned goats he produced $1H$, $2D$ and $5P$ kids: with P goats he gave $17P$, $2H$ and $1D$.

The full brother of S. Principio, Sedgemere Princeps, 1364, was hornless. He produced $25P$, $2H$ and $1D$. The closeness of number and similarity of name of these two goats has undoubtedly led to some confusion in the Herd Book; in fact, there are cases in which S. Principio is recorded in a pedigree with S. Princeps' number. These are, however, corrected in the list of errata.

In view of these considerations it is reasonable to suggest that S. Princeps was a homozygous hornless goat, while his brother, S. Principio, was a heterozygous scurred goat. Alternatively, or perhaps also, the two goats have, from time to time, been confused. If either of these possibilities be admitted, this set of exceptions to the rule that in the goat, as in cattle, polled is the dominant and horned the recessive member of a pair of Mendelian characters can be disregarded.

In addition to the data collected from the Herd Book the records of two large herds, one 80 strong, both under the personal supervision of their owners (and the importance of this observation demands no stressing) have been examined. There can be no doubt that the private records of these herds are more accurate than the Herd Book. The private records contain no entry which is in disharmony with the contention that polled and horned are a Mendelian pair, polled being the dominant. It is reasonable, therefore, to submit that the cases in the Herd Book which contradict this are instances of mistaken registration. The isolated case of Sherwood Archer, which would appear to show that a polled kid may indeed result from a horned mating, must be explained on the assumption that a mutation had occurred, or that it is a case of mistaken identity, or that the recorded sire was not its father. It may not be without significance that in the exceptional cases referred to above parents had been recently imported.

The data derived from an examination of the Herd Book in no way then contradicted the conclusion of Bateson and Saunders that the interrelationship of the horned and the hornless conditions in the goat is exactly as in cattle. It must be noted that though in cattle the polled condition is dominant there would appear to be several modifying factors involved which affect scur-development, and that the genetical significance of this has never been thoroughly examined.

That the goat should thus resemble the ox rather than the sheep in this matter is a point of some interest. The modes of inheritance of horns in cattle and sheep are very different. The goat is more closely

related to the sheep than to the ox: there are reasons for holding that goat and sheep are interfertile (Spillman, 1913, Galbusera, 1920). It is therefore a matter of some interest that there appears to be no sex-limited type of horn-inheritance in the goat as there is in the sheep. The insufficient data presented by Arkell (1912) concerning the inheritance of horns, scurs, knobs and buds in Merino crosses, though they suggest a parallelism, cannot be used in a further analysis of the data considered in this investigation.

Four-horned Goats.

Bateson (1894), quoting Gnedler (1869), describes a herd of goats on an isolated farm near Bozen. The individuals were 4-horned and this peculiarity had been inherited for many generations. In most cases the two ordinary horns were typical in shape and direction, but in addition to these, there were two lateral horns which were sickle-shaped and bent into a semicircle.

Muller (1912, 1921) observes that extra horns are not uncommon in the goat and suggests the inbreeding leads to the exhibition of the multi-horned character. Several matings were made, but the results as yet possess no clear genetical significance:

TABLE II.

Parents ♂	Parents ♀	Offspring ♂	Offspring ♀
2-horned	(*A*) 4-horned	(*B*) 4-horned	(*C*) 2-horned 2 ,, (*D*) 4 ,,
(*B*) 4 ,,	(*C*) 2 ,,	(*E*) 6 ,, (2 becoming fused) 4-horned	(*F*) 4 ,,
(*B*) 4 ,,	(*D*) 4 ,,	4 ,, 2 ,,	4 ,,
(*B*) 4 ,,	(*A*) 4 ,,	4 ,, 4 ,, 2 ,, 2 ,, 4 ,, 4 ,,	2 ,,
(*E*) 6 ,,	(*D*) 4 ,, (*F*) 4 ,,		Never more than four
4 ,,	(daughter ex F) 2-horned (dam of a 6-horned ♂) 4-horned (aunt of a 6-horned ♂)	2 ,, 4 ,, (*G*) 4 ,,	2 ,, (*H*) 4 ,, 4 ,,
(*G*) 4 ,,	(*H*) 4-horned	(*J*) 8 ,, (fusion yielding 5)	
(*J*) 8 ,,	(*H*) 4 ,,	7-horned	
(*J*) 8 ,,	2 ,, (sire 5-horned)	5 ,,	

Muller makes one statement of interest that merits further enquiry. He submits that extra horns are correlated with diminution in milk yield.

In the case of the sheep it has been noted that in breeds in which the males are 4-horned, the females are usually 2-horned. Elwes (1912) quotes the experience of a breeder who crossed 4-horned rams of the Hebridean breed to ewes of various kinds and found that all the ram lambs born were 4-horned. Wallace (1923) quotes the case of a 4-horned ram from a Manx ram and a Blackface ewe, which, when backcrossed to Blackface ewes produced offspring half of which had four horns. Very little indeed is known of the genetic nature of the multi-horned condition in either sheep or goat but such as is known would seem to suggest that in this matter they may be alike, save that in the sheep there is a sex-limited type of inheritance.

We wish to thank the officers and members of the British Goat Society for their very real help in this investigation, from which at least has emerged the fact that the Herd Book can be misleading to both breeder and geneticist. As a token of our gratitude we make the suggestion that if the breeders wish to develop a hornless breed there are indications in this paper as to the method of procedure. Any sire that is to be used must first be mated with 12 horned females. If all the offspring of these matings are polled then he can be used for breeding within the herd. If any of the offspring are horned that sire must be discarded. If this practice is consistently followed it would seem that a polled herd must be quickly established. Too little is known concerning the nature and mode of inheritance of scurs to warrant any sort of statement concerning them being made.

We wish also to thank Dr F. H. A. Marshall for the interest he has taken in this investigation.

Summary.

An examination of the Herd Book of the British Goat Society and of privately kept herd records provided strong support for the contention that, as in cattle, the polled and the horned conditions in the goat constitute a Mendelian pair of characters, polled being dominant. The data were too meagre to warrant any attempt to interpret the significance of scurs. Attention is called to the interesting fact that in this matter of horn inheritance the goat apparently resembles the ox rather than the sheep.

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ON THE PATTERN OF THE DUTCH RABBIT,

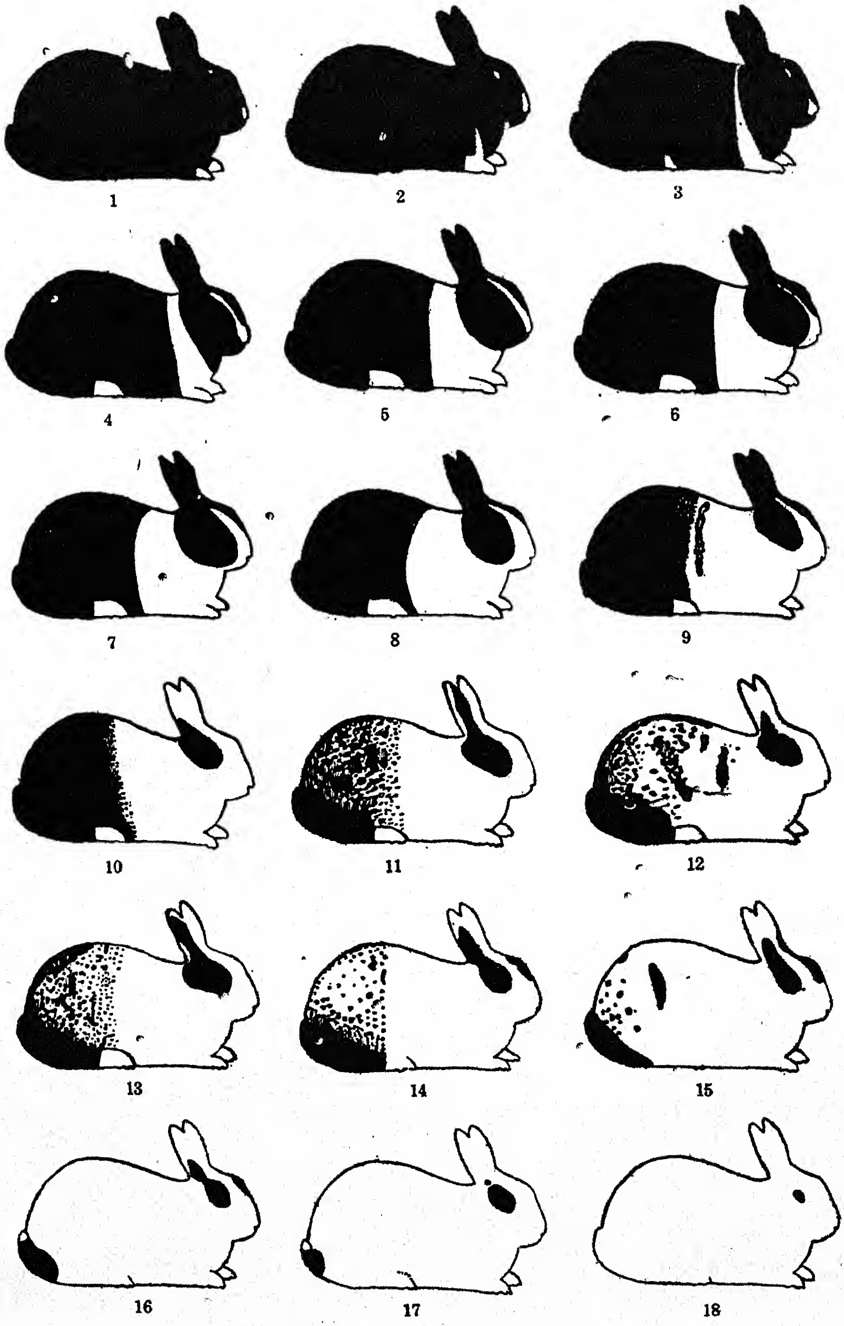
By R. C. PUNNETT, F.R.S. and M. S. PEASE, M.A.

(With Five Text-figures, Fourteen Tables, Nine Plates and Six Diagrams.)

CONTENTS

Introduction.

Ever since genetical analysis of the rabbit was first undertaken the nature of the Dutch pattern has received marked attention. The earliest records are those of Hurst (1905) who came to the conclusion that the Dutch pattern of the show type was recessive to self colour, and that the heterozygous form showed a variable but small amount of white. Subsequent breeding work however pointed to the matter being more complicated. For it was found that while certain "show" Dutch bred relatively true to the typical pattern, others threw some offspring with a considerably greater amount of white in the coat. The amount of white in these lower grades, or "Spotted Dutch" (cf. Pls. XX, XXI), showed much variation, but such animals agreed in not producing the typical Dutch pattern when bred together (Hurst, 1913). The next publication of importance was that of Castle (1919) who gave an account of his extensive experiments started in 1910. He pointed out that the typical Dutch of the shows was only one member of a long series showing a complete range from an animal which is almost entirely white to one that is almost fully self-coloured. An idea of this series is given on one



Grades 1–18 of Dutch rabbits.

Fig. 1.

of Castle's plates, here reproduced as Fig. 1. As the result of his experimental work Castle put forward the following interpretation based upon the existence of four factors forming a series of multiple allelomorphs, viz.[1]:

Du = self colour.				
du = "Dark Dutch,"	including animals of grades	1–7	in Fig. 1.
$\mathbf{du_t}$ = "Tan Dutch,"	,,	2–5	,,
$\mathbf{du_w}$ = "White Dutch,"	,,	15–17	,,

The other grades are mostly accounted for as being heterozygous forms due to various combinations of the four allelomorphs. Thus it was shown experimentally that:

$\mathbf{Dudu_w}$	are of grades	1–3
$\mathbf{Dudu_d}$	,,	0–1
$\mathbf{du_d\,du_t}$	,,	0–2
$\mathbf{du_t\,du_w}$	,,	6–9
$\mathbf{du_d\,du_w}$	,,	5–11

Shortly after its appearance, Castle's paper was criticised by one of us (R. C. P., 1920) who, though in general agreement as to the nature of the facts, had arrived at a different interpretation as the result of some years' breeding work. The alternative hypothesis put forward suggested that we are dealing with several entirely independent factors, instead of with a series of multiple allelomorphs as Castle suggested. Thus there is a range of pattern from White Dutch (Castle's grades 15–17) up to Typical Dutch (grades 7–8)[2]. Of this continuous series there are three terms that have been shown to breed approximately true, viz., White Dutch, Typical Dutch, and Spotted Dutch varying about Castle's grades 11–13. To explain this series, two factors are postulated, viz. **S** and **T**. The White Dutch possesses neither of these factors, and by the addition of either of them the pigmentation is increased, the increase being greater in animals which are homozygous for either factor than in those which are heterozygous, these latter forming various intermediate grades. The highest term in the series, viz. Typical Dutch, is produced when both **S** and **T** are present in a homozygous state. Grades of pigmentation higher than that of Typical Dutch are brought about by the operation of a distinct factor, **P**, of which the effect on any member of the series White Dutch—Typical Dutch is greatly to

[1] Castle has not himself made use of the symbols $\mathbf{du_d}$, $\mathbf{du_t}$, $\mathbf{du_w}$, but we have set them out in the accepted way in order to facilitate discussion.

[2] Though we agree with Castle that his "Tan Dutch" is a definite and distinct type we leave it out of account for the present because it does not occur in the experiments we are about to treat of. We have, however, discussed its relations below.

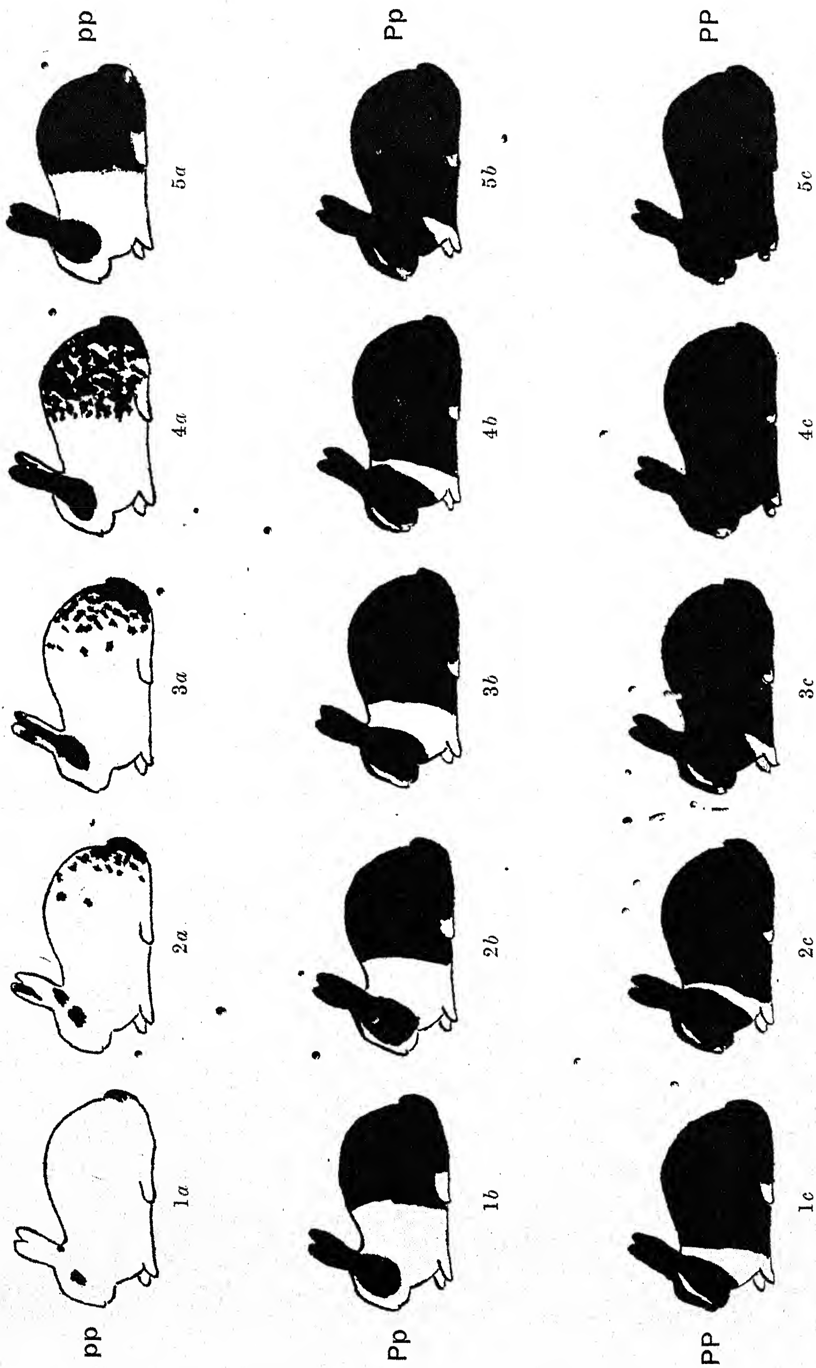


Fig. 2.

increase the amount of pigment. The effect of **P** is greater in an animal which is homozygous than in one which is heterozygous for this factor. Fig. 2 represents in simple schematic form our conception of the essential nature of this case. There is what we may call a series of basal patterns, all with much white, and ranging from White Dutch up to Typical Dutch[1]. Members of this series, which are dependent upon the distribution of factors **S** and **T**, are represented on the top line of Fig. 2, nos. 1*a*–5*a*. The addition of a single dose of **P** to each member of the series results in a great increase of pigmentation, as is represented in the middle line of Fig. 2, nos. 1*b*–5*b*. The addition of a double dose of **P** leads to some further increase in the pigmentation, so that our basal series, when also homozygous in **P**, comes to take on the form shown in Fig. 2, nos. 1*c*–5*c*.

In general terms, then, our explanation rests upon the hypothesis that pigment production is due to a series of multiple factors, whose action is more intense in the homozygous than in the heterozygous state. In addition the grade of pigmentation is markedly affected by a factor which we have termed **P**, of which the action is also inhibitive of *heterochromia iridis*[2]. The pure-breeding self-coloured rabbit is one that is homozygous for **P**, and at the same time contains several of the factors belonging to the multiple series.

Shortly afterwards a brief reply appeared from Castle (1920) in answer to the above criticism of his interpretation in terms of multiple allelomorphs, but we do not feel that it altered in any material respect the position as between the two rival hypotheses.

More recently Pap, in 1921, published an illustrated account of experiments made in Berlin. The explanation that he gives is one involving four multiple factors, $\mathbf{S}_1$, $\mathbf{S}_2$, $\mathbf{S}_3$, $\mathbf{S}_4$, each of which brings about a greater effect in the homozygous than in the heterozygous condition. The self-coloured animal is homozygous for all four factors: the less the number of factors, the less the amount of pigment, until the lowest grade of pigmentation is reached in the whitest form of White Dutch ($s_1s_1s_2s_2s_3s_3s_4s_4$). Pap further states (p. 267) that although his own experiments are explicable without the assumption of factor **P**, yet results like those of Hurst certainly point to the existence of such a factor; and he evidently regards the explanation put forward by us as

[1] Typical Dutch is the highest term in the basal series with which we have been concerned. But for reasons given later (p. 396) we regard Castle's "Tan Dutch" as a higher term in this series; and we think it likely that there may be yet higher terms, possibly ranging even up to a self-coloured animal.

[2] Cf. note below, p. 382, *note*.

more consistent with his own results than the hypothesis of multiple allelomorphs favoured by Castle. Pap's views are in no way inconsistent with our own if we regard the more heavily pigmented forms which appeared in his experiments as higher terms in our so-called "basal series." For this, as we have already hinted, may quite possibly range even up to self colour. We are, however, not quite satisfied as to the complete absence of factor **P** from his material, but his results are not presented in such a way that we can test his data for this point.

Earlier Work.

Before passing on to the account of our experiments we may give a brief outline of the circumstances that led up to them. The choice of the Dutch pattern in the rabbit was made by one of us (R. C. P.) in 1907, and crosses were made between typical animals of this variety and Himalayan rabbits (cf. Pedigree no. 4). But though the experiments were started with this idea the appearance of unusual phenomena connected with colour inheritance led to the breeding work being primarily directed to their elucidation. Records of the pattern were kept, but for several years little advance was made towards understanding its genetical nature. During this time the main facts elucidated were (1) that Dutch × self colour gave in general F_1 animals with a small amount of white marking, and even occasionally a self-coloured animal, (2) that the F_2 generation was complex, and (3) that some Dutch might throw a lower grade form, "Spotted Dutch," as recessive.

In 1911 a series of experiments was started on the inheritance of weight in rabbits, of which the results were subsequently published in this *Journal* (Punnett and Bailey, 1918). By crossing Spotted Dutch, already found to breed fairly true, with the self-coloured Flemish Giant it was hoped to obtain data bearing on the inheritance of the Dutch pattern as well as upon the inheritance of weight. Since weight was the main object of the enquiry, the pattern data must be regarded as a bye-product. It was, however, established that "Spotted Dutch"[1] × self coloured gave white marked animals in F_1, and in F_2 a range from self coloured down to White Dutch[2]. Further, some self-coloured animals were raised in F_2 and F_3 which, when bred together, gave nothing but self-coloured progeny.

[1] Some of these "Spotted Dutch" were of a rather low grade of pigmentation of the type we later distinguished as "Reduced Spotted Dutch" (R.S.D.). It was these that we used for crossing with the Flemish Giant.

[2] The appearance of White Dutch was doubtless due to the fact that it was carried by the Spotted Dutch used which were of low grade.

After the conclusion of our preliminary experiments on the inheritance of weight more hutch room was available, and we began to pay more attention to the pattern case. We established strains of Typical Dutch, of Spotted Dutch, and of White Dutch, of which a detailed account will be found in the Appendix to this paper. From the results of crossing these forms with one another and with self-coloured animals, and especially from the results obtained by crossing White Dutch back to various extracted pattern forms, we were led to formulate the hypothesis published by one of us in connection with a criticism of Castle's paper, and already given in outline above. We do not propose to give any detailed account of these earlier experiments, except in so far as they bear directly upon the later and more critical work begun in 1920. This consists of two portions, viz. a cross between Typical Dutch and White Dutch undertaken to verify our original hypothesis, and a cross between Typical Dutch and what we have termed "Deep Dutch," devised as a crucial test between Castle's hypothesis and our own. These two parts we may take in order.

The Cross Typical Dutch[1] × White Dutch.

From this cross F_1 animals are of the type we have termed "Reduced Spotted Dutch," more or less intermediate between the two parental forms (cf. Pl. XXI, fig. 5). Of such animals 5 ♀♀ and 2 ♂♂ were used to produce an F_2 generation consisting of 98 individuals (cf. Table I).

TABLE I.

	D.	S.D.	R.S.D.	R.S.D. / V.R.S.D.	V.R.S.D.
♀R 35 × ♂R 34	—	12	12	5	1
♀R 35 × ,,	2	14	16	1	—
♀R 76 × ,,	1	2	8	2	1
♀R 77 × ,,	—	2	5	2	2
♀Q 34 × ♂Q 32	2	2	3	1	2
Total	5	32	44	11	6

Note. The relationship of the animals used will be found in Pedigree 4, p. .

It formed a fairly continuous series ranging between White Dutch and Typical Dutch, there being nothing more heavily pigmented than the latter. In practice we distinguished the following five grades, though we

[1] Details with regard to the material used will be found in the Appendix (pp. 398–405). We may say here that the majority of our Typical Dutch strain were of grades 7–8, and that the most extreme variations did not fall outside grades 6 and 9. We pass over irregularities of outline and the small coloured patches that may appear in the white area.

should say that these classes were originally established on purely empirical grounds for the sake of convenience.

	Abbreviation	Approximate grade in Fig. 1	Average near
α White Dutch[1] (= very Reduced Spotted Dutch)	V.R.S.D.	16–17	Fig. 2 No. 1*a*
β Intermediate grade between 1 and 2	R.S.D. / V.R.S.D.	15	,, No. 2*a*
γ Reduced Spotted Dutch	R.S.D.	13–14	,, No. 3*a*
δ Spotted Dutch	S.D.	10–12	,, No. 4*a*
ε Typical Dutch	D.	7–9	,, No. 5*a*

The distribution of the 98 F_2 animals among these five classes was as follows:

D.	S.D.	R.S.D.	R.S.D. / V.R.S.D.	V.R.S.D.
5	32	44	11	6

We account for this distribution by supposing that we are concerned with two factors, **S** and **T**, of which the presence of either in the zygote leads to an increase in the amount of pigmentation. In order to cover our results we must suppose that although these two factors act in a similar manner, one of them (**S**) acts with rather greater intensity than the other (**T**).

Since on our hypothesis the F_1 animals must be of the constitution **SsTt**, the nature of the expected F_2 generation is given in the usual way in Fig. 3.

To the zygotic composition in each square we have added the abbreviation signifying the class to which we should expect any given

[1] Any of these forms may exhibit *heterochromia iridis* due to the partial or complete disappearance of the brown pigment in the outer layer of the iris. The *heterochromia* shows great variations, from a small patch of light blue in one eye to completely blue eyes on both sides. Generally speaking the *heterochromia* is more marked according as the animal belongs to a lower grade of pigment. We give some figures for a number of animals belonging to the different classes.

Typical Dutch	with normal eyes		34;	with heterochromia		79
Spotted	,,	,,	38;	,,	,,	36
R.S.D.	,,	,,	14;	,,	,,	70
R.S.D. / V.R.S.D.	,,	,,	1;	,,	,,	23
V.R.S.D.	,,	,,	0;	,,	,,	61

We never met with a White Dutch having normal eyes, and only once with one of the next grade above. It is curious that the proportion of normal eyes among Spotted Dutch is higher than among Typical Dutch. We are inclined to believe that *heterochromia* is associated with the amount of white on the head—the more white there exists on the head the more likely the animal is to show *heterochromia*, due, as it were, to the invasion of the ocular area by white. We have never met with a single case of any trace of *heterochromia* in an animal containing **P**.

ST **ST** D.	**ST** **St** S.D.	**ST** **sT** S.D.	**ST** **st** R.S.D.
St **ST** S.D.	**St** **St** S.D.	**St** **sT** R.S.D.	**St** **st** R.S.D.
sT **ST** S.D.	**sT** **St** R.S.D.	**sT** **sT** R.S.D.	**sT** **st** $\frac{\text{R.S.D.}}{\text{V.R.S.D.}}$
st **ST** R.S.D.	**st** **St** R.S.D.	**st** **sT** $\frac{\text{R.S.D.}}{\text{V.R.S.D.}}$	**st** **st** V.R.S.D.

Fig. 3.

animal to belong. It will be noticed that we make no phenotypical distinction between **SSTt** and **SStt** animals, or between **SsTt** and **Sstt** animals, because we suggest that the effect of **T** is less than that of **S**, and that in the presence of **S** a single dose of **T** will not increase the pigmentation sufficiently to distinguish such animals from those which lack **T**. It must be remembered that the various grades are purely empirical, and tend to merge into one another. On this hypothesis the expected proportions of our 5 empirical classes are

$$1\,\text{D.} : 5\,\text{S.D.} : 7\,\text{R.S.D.} : 2\,\frac{\text{R.S.D.}}{\text{V.R.S.D.}} : 1\,\text{V.R.S.D.}$$

and, as the following figures show, this expectation is closely realised in our actual figures:

	D.	S.D.	R.S.D.	$\frac{\text{R.S.D.}}{\text{V.R.S.D.}}$	V.R.S.D.
Actual	5	32	44	11	6
Expectation	*6·1*	*30·6*	*42·9*	*12·3*	*6·1*

We may add that we made a further test of our hypothesis by crossing F_1 animals with our strain of Typical Dutch. Since the gametes produced by the latter are, on hypothesis, all of the nature **ST**, we should expect the animals produced from such matings to fall into the three classes D., S.D., and R.S.D. in the ratio 1 : 2 : 1. Of the 27 animals bred in this way 7 were Dutch, 18 Spotted Dutch, and 2 were R.S.D. Only the three expected classes appeared, and the Typical Dutch came in the expected proportion. There was however a distinct deficiency of R.S.D. animals, though, in view of the small numbers bred, this may have been a chance result.

We have spoken of **S** and **T** as multiple factors, though were we dealing with multiple factors in the strict sense we should expect our five classes to show a symmetrical curve, appearing in the ratio 1 : 4 : 6 : 4 : 1, provided that we had classified them in accordance with their genetical composition. The actual curve is however clearly a skew one, with greater numbers towards the more heavily pigmented end. Therefore we must suppose either that the intermediate classes arbitrarily chosen do not correspond exactly with the genetical classes, or else that our two factors are not of the same value, and therefore that they are not, strictly speaking, multiple factors. On the evidence we do not consider it possible to decide definitely between these two views; nor is it a point of very great importance here. The essential feature of our interpretation is that the series of patterns ranging between White Dutch and Typical Dutch depends upon two independently segregating factors, acting in the same sense, and each producing a greater effect in the homozygous than in the heterozygous state. With this essential feature the main facts of the experiment are in accordance. For from the two pure strains we obtain an F_1 generation of intermediate grade; the F_2 generation consists of a series ranging between the two parental forms; and the two parental forms, which alone can be recognised with certainty, each reappear in the expected ratio of 1 in 16.

It is of course clear that the results of this experiment are definitely opposed to the view that Typical and White Dutch are due to two of a series of multiple allelomorphs as suggested by Castle. For on this view the F_2 generation should consist of Typical Dutch, intermediates similar to F_1 (R.S.D.), and White Dutch in the ratio 1 : 2 : 1. Were Castle's suggestion adopted we must also suppose that the two strains crossed differed also in one or more factors through the operation of which the amount of pigment was either increased or decreased. Although an explanation of this particular set of experiments is feasible on such lines it is obvious that nothing is to be gained on grounds of economy of hypothesis. There are however rabbits, Dutch in appearance, whose genetical behaviour with respect to White Dutch, would at first sight appear to support Castle's suggestion of multiple allelomorphs. The nature of these may now proceed to discuss.

The "Mock Dutch" Rabbit.

We have already mentioned (p. 380) that among the earlier experiments an F_2 generation was raised from a cross between Flemish Giant, a pure self-coloured breed, and some R.S.D. animals. The F_1 animals

showed a rather variable amount of white markings, though all of them were much more heavily pigmented than Typical Dutch. Owing to the fact that all of the animals had to be kept to maturity in order to obtain a record of their weight curves, only a small F_2 generation was raised. The 53 animals whose pattern was recorded exhibited an apparently continuous range of pigmentation from self coloured down to R.S.D. By this time the conception of the factor we have called **P** had begun to take shape, and as a strain of White Dutch had been established it was decided to test for the existence of **P** in the following manner. **P** must have been brought into the cross by the Flemish parent since the Dutch and Spotted Dutch used did not throw the higher grades of pigmentation. F_1 animals ex Dutch × Flemish must therefore be heterozygous for **P**, however constituted for other factors. By a series of appropriate back crosses with White Dutch on F_1 animals, and subsequently on their derivatives, we should expect eventually to obtain rabbits heterozygous for **P** on a basis of homozygous White Dutch. It was argued that such animals should be easily recognisable by their breeding behaviour, for when mated with White Dutch they should give only White Dutch and animals similar to themselves in approximately equal numbers.

The details of the experiment may be gathered from Pedigree no. 1 (p. 407). Two F_1 does, O 223 and P 17, were mated to the White Dutch buck G 196[1]. In either case the progeny fell into two distinct groups. Of the 15 young from O 223, 8 were towards self colour, though with a variable amount of white marking, while 7 were light, varying from R.S.D. to V.R.S.D. On the 7 young from P 17 five were dark and two were light. Since the dark forms alone could contain the postulated **P** factor, two of these, viz. ♂ Q 29 and ♀ Q 31, were chosen for crossing back again to White Dutch. ♂ Q 29 mated with the White Dutch ♀ Q 90 gave only two young, viz. 1 White Dutch, and one resembling Typical Dutch, viz. ♀ Q 137. ♀ Q 31 was mated back to her White Dutch father and in 3 litters gave 12 young of whom 6 were dark with a variable amount of white marking, 1 was Typical Dutch in appearance, and 5 ranged from R.S.D. to V.R.S.D. The animal resembling a Typical Dutch was subsequently bred from and figures in Pedigree 1 as ♀ Q 107. Since the least heavily pigmented animals belonging to the dark group of the progeny from Q 31 and Q 29 when mated to White Dutch were Typical Dutch in appearance it was probable that these were the desired animals, viz. animals heterozygous for **P** on a basis of White Dutch. As they

[1] For a photograph of this animal see *Journ. Gen.* Vol. IX. Pl. XI, Fig. 2.

were both does they were both mated back to ♂ G 196 to test this point. In several litters from this mating ♀ Q 137 gave 11 animals like Typical Dutch in appearance, 11 White Dutch, and nothing else. From the other doe, Q 107, 9 offspring were born, of which 3 were like Typical Dutch, and 6 were White Dutch.

These animals, of Typical Dutch appearance, but genetically heterozygous forms of the constitution **Ppsstt** on our hypothesis, we have termed "Mock Dutch" to distinguish them from the true breeding Typical Dutch of the constitution **ppSSTT**. Besides the "Mock Dutch" referred to above we have bred other animals of similar appearance and constitution which we have tested by crossing with White Dutch. Some of the results from these animals, whose breeding can be gathered from Pedigree no. 1, are now given in Table II.

TABLE II.

		M.D.	V.R.S.D.
♀R 20 (M.D.)	× ♂Q 189 (V.R.S.D.)	6	4
♀Q 188 (V.R.S.D.)	× ♂R 21 (M.D.)	1	1
♀R 52 (M.D.)	× ♂Q 189 (V.R.S.D.)	2	3
♀Q 166 (V R.S.D.)	× ♂R 53 (M.D.)	1	—
♀R 78 (V.R.S.D.)	× ,,	1	2
♀Q 188 (V.R.S.D.)	× ♂R 60 (M.D.)	2	2
♀R 78 (V.R.S.D.)	× ,,	2	3
♀R 79 (M.D.)	× ♂R 50 (V.R.S.D.)	1	5
♀R 78 (V.R.S.D.)	× ♂R 99 (M.D.)	2	4
♀R 181 (V.R.S.D.)	× ♂R 100 (M.D.)	5	5
,,	× ♂R 240 (M.D.)	2	3
		25	32

From all of these matings only the expected two classes of offspring, viz. Mock Dutch (M.D.) and White Dutch (V.R.S.D.) were produced, and the proportion in which they appeared were not far removed from the postulated 1 : 1 ratio. As in any other type of Dutch, there is some range of variation in Mock Dutch, but this is not greater than among Typical Dutch. Some examples of Mock Dutch rabbits are shown on Pl. XVI, figs. 1–5, while Pl. XXII offers a graphic representation of the striking segregation exhibited by the two classes of offspring from the cross between Mock and White Dutch. We may add that in such families we have found that all of the White Dutch exhibit *heterochromia iridis*, though no trace of this has appeared in any Mock Dutch rabbit.

The "Deep Dutch" Rabbit.

On our hypothesis the factor **P** should give rise to a more heavily pigmented state in homozygous than in heterozygous animals. Consequently the next stage in the enquiry was to breed these Mock Dutch

animals together in order to ascertain the appearance of the homozygous animal of the constitution **PPsstt**. For this purpose 4 does (Q 107, Q 137, Q 195 and R 52), and three bucks (Q 196, Q 224*e* and R 60) were mated as shown below in Table III and on Pedigree no. 2 (p. 408):

TABLE III.

	Deep Dutch	Mock Dutch	White Dutch
♀Q 107 × ♂Q 196	—	1	1
♀Q 137 × ♂Q 224*e*[1]	—	2	2
,, × ♂Q 196	3	3	5
♀Q 195 × ♂Q 196	6	5	3
,, × ♂ R 60	—	2	—
♀R 52 × ,,	4	7	7
	13	20	18

The progeny fell into three distinct classes, viz. White Dutch, Mock Dutch, and Dutch marked animals more heavily pigmented than the Mock Dutch class. For this darker class we have used the term "Deep Dutch," and they are presumably of the constitution **PPsstt**. The white markings of Deep Dutch frequently show some asymmetry, but the class as a whole may be described as approximating to grade 4 of Fig. 1. Some examples of Deep Dutch will be found figured on Pl. XIX. When mated with White Dutch they gave only Mock Dutch offspring as shown in Table IV:

TABLE IV.

♀R 19	× White Dutch ♂	gave 11	Mock Dutch
♀R 80	× ,, ,,	,, 3	,, ,,
♀R 101	× ,, ,,	,, 5	,, ,,
White Dutch ♀	× ♂T 93	,, 3	,, ,,
,, ,,	× ♂T 94	,, 1	,, ,,
,, ,,	× ♂T 95	,, 3	,, ,,

When bred together Deep Dutch produced only offspring of similar nature. As indicated in Pedigree no. 1, 22 rabbits were bred in this way from two does, R 19 and R 80, and two bucks R 207 and T 93. They showed some range of variation, from grade 3 to grade 5, but may be said, like their parents, to have centred about grade 4.

Although of the same average grade, these Deep Dutch rabbits must not be confused with Castle's "Tan" Dutch, but for the following reasons must be regarded as quite distinct: (1) though the amount of white is about the same in the two classes its distribution is rather different; for the blaze is consistently wider in "Tan" Dutch. (2) Probably associated with this is the fact that while *heterochromia iridis* may occur

[1] This was a Mock Dutch animal, ex ♀ Q 137 × ♂ G 196.

in "Tan" Dutch we have never found it in any animal either of the Deep or Mock Dutch classes. (3) When crossed with White Dutch, "Tan" Dutch gives in F_2 a result quite different to that given by Deep Dutch. For instead of producing only the three well-marked groups Deep, Mock and White Dutch it gives a continuous series ranging between grades 3–14. Again the F_1 animals ex Tan Dutch × White Dutch, when crossed back to White Dutch, give a continuous series ranging between grades 7–17, instead of equal numbers of Mock and White Dutch (cf. Castle, 1919, Text-fig. 4, p. 13).

The cross Deep Dutch × Typical Dutch.

The possession of the two true breeding strains, Deep Dutch and Typical Dutch, gave us the opportunity of making a crucial experiment to decide between Castle's hypothesis of multiple allelomorphs and our own hypothesis of separate factors. The data we have just set out in connection with Deep Dutch and White Dutch are, taken by themselves, as compatible with Castle's hypothesis as with our own. And, with the assumption of modifying factors, it is possible to argue a case for regarding White Dutch and Typical Dutch as allelomorphic. If this view is taken we must regard Deep Dutch, Typical Dutch and White Dutch, as being all three in the same series, and all three allelomorphic to one another. Hence if we cross Deep Dutch with Typical Dutch we should expect an F_1 generation of intermediate nature, and an F_2 generation ranging between the extremes of variability exhibited by the two parental forms, *i.e.* between grades 3–8. There should be no animals which were self coloured or near it, nor should there be any which fell into the White or Spotted Dutch categories.

But on the hypothesis of separate factors, which we have put forward, a very different result is to be looked for from this cross. F_1 animals would be of the constitution **PpSsTt**, and in appearance nearly as heavily pigmented as the Deep Dutch parent (cf. Fig. 1, 3 *b* and 1 *c*). Bred together such F_1 animals should give an F_2 generation consisting of a continuous series ranging from White Dutch (**ppsstt**) up to **PPSSTT** animals, which we should expect to be almost, if not completely self-coloured.

We may now turn to the experimental data. Several matings were made between Deep Dutch and Typical Dutch, of which the details will be found in Pedigree no. 3. Other similarly constituted animals were made by crossing Mock Dutch with Typical Dutch, a mating which gave **PpSsTt** animals and rabbits of the R.S.D. type in approximately equal numbers. Altogether 67 F_1 animals were raised in either

one or other of these two ways. They showed a good deal of variation, ranging from about grade 5 up to about grade 2, and averaging about grade 3. In the highest grade of pigmentation one side was generally more pigmented than the other, giving the impression of an animal with a fair amount of white (*e.g.* grade 4) in which mismarking obscured the white on one side. Some idea of the class may be obtained from those figured on Pl. XVII, figs. 1–6. The average pigmentation of these animals then was rather higher than that of the Deep Dutch, as indeed we had anticipated before we made the cross.

From various of these F_1 does with 2 F_1 bucks a large F_2 generation of over 500 animals was raised of which the details are set out in Table V below.

TABLE V.

F_1 ♂ R 204

F_1 ♀	Self	A.S.	D.T.S.	D.D.	D.	S.D.	R.S.D.	R.S.D./V.R.S.D.	V.R.S.D.
R 203	—	4	21	8	8	7	3	—	2
T 16	—	17	15	8	9	4	7	4	—
T 17	—	5	10	4	5	5	9	4	1
T 42	—	—	12	3	5	2	1	3	—
T 50	—	3	6	—	1	1	—	—	—
T 78	—	2	4	—	2	—	4	3	1
T 79	—	3	10	1	8	1	4	1	3
T 106	—	—	7	2	2	4	2	1	—
T 176	—	2	5	1	1	—	—	—	—
T 177	—	3	6	1	—	1	—	—	—
T 218	—	2	—	—	2	1	2	—	1
T 220	—	1	2	—	2	1	—	—	—
T 221	—	1	8	—	2	2	1	—	—
T 222	—	1	7	5	3	1	1	1	—
U 233									
U 234									
U 235									
Total	328	44	113	33	49	30	34	17	8
		44	146		49	30	34	17	8
Exp.		*51*	*154*		*46*	*26*	*36*	*10*	*5*

F_1 ♂ T 35b

F_1 ♀	S.	A.S.	D.T.S.	D.D.	D.	S.D.	R.S.D.	R.S.D./V.R.S.D.	V.R.S.D.	
R 203										
T 16	—	—	4	5	—	—	3	—	—	
T 17	—	7	7	3	1	2	—	—	—	
T 42										
T 50	—	5	7	5	—	4	2	—	—	
T 78	—	2	6	—	4	1	2	1	—	
T 79	—	1	9	—	2	4	—	—	—	
T 106	—	1	9	3	1	1	3	—	—	
T 176	—	3	1	—	1	1	—	—	—	
T 177	—	2	13	1	2	4	—	—	—	
T 218	—	8	14	3	—	3	4	—	—	
T 220	—	1	7	3	—	—	—	—	—	
T 221										
T 222										
U 233	—	5	5	1	—	3	—	—	—	
U 234	—	6	6	1	—	8	1	—	—	
U 235	—	2	7	1	—	—	1	—	—	
Total	—	43	95	26	11	31	16	1	—	Total 223
	—	43	121		11	31	16	1		
Exp.	—	*35*	*106*		*31*	*17*	*24*	*7*	*3*	

	S.	A.S.	D.T.S./D.D.	D.	S.D.	R.S.D.	R.S.D./V.R.S.D.	V.R.S.D.	
Sum	—	87	267	60	61	50	18	8	=551
Expectation	*9*	*78*	*259*	*78*	*43*	*60*	*17*	*9*	
	(1)	(9)	(30)	(9)	(5)	(7)	(2)	(1)	

This F_2 generation showed a full range of variation from White Dutch up to animals which were fully self coloured save for a few white hairs at the tip of the nose or muzzle, or on the tip of a fore paw. The

nature of this generation is clearly opposed to the hypothesis that we are dealing with members of a series of multiple allelomorphs; for that hypothesis not only fails to explain the great range of variation, but is at once negatived by the appearance of the White Dutch animals.

On the other hand, since the F_1 animals are on our hypothesis heterozygous for all of the 3 factors **P**, **S**, and **T**, the general nature of this F_2 generation is what we were led to expect. The question between an interpretation in terms of a series of multiple allelomorphs and one in terms of separate and independent factors we consider to be definitely settled by this experiment in favour of the latter, and we may now enquire how far the actual details are explicable on our hypothesis involving the three factors **P**, **S**, and **T**, exerting each the specific action we have already ascribed to them on the basis of other facts.

On our hypothesis the F_1 animals, being of the constitution **PpSsTt**, must be producing equal numbers of the 8 types of gamete **PST**, **PSt**, **PsT**, **Pst**, **pST**, **pSt**, **psT**, **pst**[1]. On Fig. 4 is set out in the usual way the nature of the F_2 generation to be expected.

	PST	PSt	PsT	Pst	pST	pSt	psT	pst
PST	Self	A.S.	A.S.	A.S.	D.T.S.	D.T.S.	D.T.S.	D.T.S.
PSt	A.S.	A.S.	A.S.	D.T.S.	D.T.S.	D.T.S.	D.T.S.	D.T.S.
PsT	A.S.	A.S.	D.T.S.	D.T.S.	D.T.S.	D.T.S.	D.	D.
Pst	A.S.	D.T.S.	D.T.S.	D.T.S.	D.T.S.	D.T.S.	D.	D.
pST	D.T.S.	D.T.S.	D.T.S.	D.T.S.	D.	S.D.	S.D.	R.S.D.
pSt	D.T.S.	D.T.S.	D.T.S.	D.T.S.	S.D.	S.D.	R.S.D.	R.S.D.
psT	D.T.S.	D.T.S.	D.	D.	S.D.	R.S.D.	R.S.D.	R.S.D. / V.R.S.D.
pst	D.T.S.	D.T.S.	D.	D.	R.S.D.	R.S.D.	R.S.D. / V.R.S.D.	V.R.S.D.

Fig. 4.

The lower 16 squares on the right hand, being the product of two similar series of gametes **pST**, **pSt**, **psT**, **pst**, are strictly comparable with the F_2 generation from Typical × White Dutch already set out in Fig. 3, p. 383, and similar phenotypical designations have consequently been given. Again we know that animals of the constitution **Ppsstt** are

[1] Assuming of course that there is no linkage between any of these factors.

Mock Dutch, and since, on hypothesis, **T** produces little effect apart from **S**, we may suppose that animals of the constitutions **PpssTT** and **PpssTT** also fall within the limits of the Typical Dutch type of pattern. Of the rest we must suppose that animals which are homozygous for **P** and at the same time contain **S** are nearly, if not quite, self coloured (= A.S.); and of such there are 10 in the figure. This accounts for 34 out of the 64 squares in Fig. 4. Of the remaining 30 seven are homozygous for **P** but do not contain **S**, while 23 are heterozygous for **P** but also contain **S**. All of these must consist of animals which are more heavily pigmented than the upper limit of Typical Dutch, and yet with more white than an animal which we have classed as almost self (A.S.). Roughly these 30 squares should be covered by grades 2–4 (Fig. 1). Owing to the small amount of white it is impossible to separate them without elaborate breeding tests and we have therefore classed them all together as "Dark Dutch towards self" (= D.T.S.). On our hypothesis then this F_2 generation should fall into the following 7 classes, and in the following proportions:

Almost self (A.S.)	10	64
Dark Dutch towards self (D.T.S.)	30	
Dutch (D.)	9	
Spotted Dutch (S.D.)	5	
Reduced Spotted Dutch (R.S.D.)	7	
R.S.D.—V.R.S.D. $\left(\frac{\text{R.S.D.}}{\text{V.R.S.D.}}\right)$	2	
White Dutch (V.R.S.D.)	1	

The actual experimental results, as compared with expectation, are as follows:

	A.S.	D.T.S.	D.	S.D.	R.S.D.	$\frac{\text{R.S.D.}}{\text{V.R.S.D.}}$	V.R.S.D.
Actual	87	267	60	61	50	18	8
Expectation	*87*	*259*	*78*	*43*	*60*	*17*	*9*

The most marked discrepancies between the calculated and the actual results are to be found among the classes D., S.D., and R.S.D. On the other hand the end terms A.S., D.T.S., $\frac{\text{R.S.D.}}{\text{V.R.S.D.}}$, and V.R.S.D. conform closely to expectation. Having regard to the difficulties in classifying a series of intergrading forms we are inclined to lay more stress upon the conformity of the end terms than upon divergencies among the middle ones, and we consider that this F_2 generation taken as a whole bears out the hypothesis which we have put forward.

As regards the existence and mode of operation of factor **P** we consider the data conclusive. The four classes S.D., R.S.D., $\frac{\text{R.S.D.}}{\text{V.R.S.D.}}$

and V.R.S.D. are of course all **pp** in constitution, while of the Dutch class (D.) 1 in 9 only must be supposed to be **ppSSTT** in constitution, the remaining 8 being Mock Dutch in nature and heterozygous for **P**. If therefore we reckon 7 of our 60 Dutch as lacking **P**, we obtain, out of our total of 551, 146 without **P** and 405 with this factor—a fairly close approach to the expected 3 : 1 ratio.

But although the data from this cross are generally in accordance with our hypothesis they present a feature which points to some disturbing cause that has escaped our analysis. In the production of the F_2 generation only 2 F_1 bucks were used, viz. R 204 and T 35*b*. The results from these two bucks are set out apart in Table V, p. 389, where it will be noticed that there is a definite difference between them. As compared with the calculated series, that from R 204 is shifted on the scale a little towards the lower grade, *i.e.* in the V.R.S.D. direction, whereas the series from T 356 is shifted somewhat towards the higher grade, *i.e.* in the direction of self colour. A fairer comparison between the two animals is to be obtained if we take into account their performances with the same series of does, as in Table VI.

TABLE VI.

	F_1 ♂ R 204							F_1 ♂ T 35*b*						
F_1 ♀	A.S.	D.T.S. D.D.	D.	S.D.	R.S.D.	R.S.D./V.R.S.D.	V.R.S.D.	A.S.	D.T.S. D.D.	D.	S.D.	R.S.D.	R.S.D./V.R.S.D.	V.R.S.D.
T 16	17	23	9	4	7	4	—	—	9	—	—	3	—	—
T 17	5	14	5	5	9	4	1	7	10	1	2	—	—	—
T 50	3	6	1	1	—	—	—	5	12	—	4	2	—	—
T 78	2	4	2	—	4	3	1	2	6	4	1	2	1	—
T 79	3	11	8	1	4	1	3	1	9	2	4	—	—	—
T 106	—	9	2	4	2	1	—	1	12	1	1	3	—	—
T 176	2	6	1	—	—	—	—	3	1	1	1	—	—	—
T 177	3	7	—	1	—	—	—	2	14	2	4	—	—	—
T 218	2	—	1	1	2	—	1	8	17	—	3	4	—	—
T 220	1	2	2	1	—	—	—	1	10	—	—	—	—	—
	38	82	31	18	28	13	6	30	95	11	20	14	1	—
Expect.	*33*	*101*	*31*	*17*	*24*	*7*	*3*	*28*	*85*	*25*	*14*	*20*	*6*	*3*

When this is done the divergence between the performance of the two animals is not quite so marked, but it is nevertheless clearly evident. To account for it we can only suggest that we may be dealing with some further factor of which the action on pigmentation of the coat is similar to that of **S** and **T**, but less powerful than in either of these. It is conceivable that such a factor may have been brought in by the White Dutch. That White Dutch mated among themselves produce only

White Dutch is true, but we must remember that there is some variation even among them, and it may be possible that this is connected with a factor hitherto undetected. Where the pigment is very small in amount, as in White Dutch, even a 50 per cent. increase in it would not appear striking; and among the animals we have classed as White Dutch some have at least twice as much pigment as others. When, however, such a difference, actually small though relatively large, is magnified, as it were, through the introduction of other factors, a marked difference may result among the grades of pigmentation higher than that of White Dutch.

We suggest then the possibility of T 35*b* differing from R 204 in containing a factor of this nature. If so we should expect also to find similar differences among the does. The number of young from individual does is too small to compare them directly with one another; but we can make a rough test by selecting those does which, with one buck, show a tendency to produce more pigmented offspring, and examine whether they show a similar tendency with the other buck. Thus the four does T 50, T 176, T 177, and T 220, when mated with R 204 gave no offspring below the grade S.D. Table VII shows the offspring of these four does from T 35*b* as compared with the offspring of the remaining does in Table VI from the same buck.

TABLE VII.

	A.S.	D.T.S.	D.	S.D.	R.S.D.	$\frac{\text{R.S.D.}}{\text{V.R.S.D.}}$	
T 50, T 176, T 177, T 220	11	37	3	9	2	—	(= 62)
T 16, T 17, T 78, T 79, T 106, T 218	19	58	8	11	12	1	(=119)

From these figures it is clear that the four does selected owing to their tendency to produce more pigmented offspring with R 204, tend also to produce more pigmented offspring with T 35*b*. Reference to Table VI shows that the three does U 233, U 234, U 235 also tend to produce more pigmented progeny with T 35*b*, but were not mated with R 204. On the other hand a tendency in the opposite direction is noticeable with ♀ R 203 when mated with R 204, whereas this doe was not mated with T 35*b*. In other words a higher proportion of does with a tendency to produce offspring of heavier pigmentation was mated with ♂ T 35*b* than with ♂ R 204, and this has served to accentuate the difference observed in Table VI between the performances of these two bucks.

The F_3 Generation.

Before we started the cross between Deep Dutch (**PPsstt**) and Typical Dutch (**ppSSTT**) we were prepared to find a small proportion of self-coloured animals in the F_2 generation. For we thought that the **PPSSTT** animals would probably be self coloured in appearance. This expectation was not realised. Although 9 self-coloured animals might have been looked for in an F_2 generation of 551, not one was actually found. Some of the F_2 animals however were self coloured except for a small fleck of white, generally on the tip of the nose or the muzzle, though occasionally on the tip of a fore paw. The natural deduction is that the action of **P**, even in rabbits homozygous for the factor, is not quite strong enough to bring a rabbit of the constitution **SSTT** into the completely self-coloured class.

Since it was possible, though most unlikely, that the **PPSSTT** animal had not appeared in the F_2 generation we determined to test the point further by selecting some of the F_2 animals with the smallest amount of white markings, and breeding these together. As such animals would be homozygous for **P**, and at the same time either **SSTT**, **SSTt**, or **SsTT** in constitution they should give a good proportion of **PPSSTT** progeny. From 9 does and 5 bucks 120 young were bred, and the details are given in Table VIII. Some of these F_2 animals will be found illustrated on Pl. XVIII, figs. 1–6.

TABLE VIII.

		A.S.	D.T.S.
♀U 63*b*	× ♂U 96	5	—
,,	× ♂U 159*a*	6	—
♀U 74*c*	× ♂ ,,	5	—
,,	× ♂U 159*b*	6	—
,,	× ♂U 184*a*	6	—
♀U 98	× ♂U 96	6	—
,,	× ♂U 97	9	—
,,	× ♂U 159*a*	7	1
♀U 99	× ,,	7	—
,,	× ♂U 96	3	—
,,	× ♂U 97	7	—
♀U 100	× ,,	2	3
,,	× ♂U 96	11	—
,,	× ♂U 159*a*	6	—
♀U 101	× ♂U 96	5	—
♀U 157*c*	× ,,	3	—
,,	× ♂U 159*b*	2	2
♀U 231	× ,,	3	—
,,	× ♂U 97	2	—
♀U 232	× ♂U 159*a*	7	1
		113	7

Not a single fully self-coloured animal appeared in this F_3 generation, though, as in the preceding generation, a few showed only a very small trace of white. Of the 120 young 113 were recorded as almost self (A.S.), resembling the parents. The other 7 young showed a rather lower grade of pigmentation, towards, though rather deeper than the Deep Dutch type characteristic of **PPsstt** animals. Such animals must be supposed not to contain **S**, though **T** is almost certainly present. To account for their presence we must suppose that both of the parents in such cases were heterozygous for **S**. In the production of the four litters in which these 7 Deep Dutch appeared, seven parents were concerned, viz. ♀♀ U 98, U 100, U 157*c*, U 232, and ♂♂ U 97, U 159*a*, U 159*b*. Of these 7 animals four, viz. ♀♀ U 100, U 157*c*, U 232 and ♂ U 159*a*, have also been crossed with White Dutch, as were also certain other of these F_3 rabbits. The results are shown in Table IX.

TABLE IX.

		D.T.S.	D.D.	D.
♀U 63*b*	× V.R.S.D.	—	3	—
♀U 74*c*	× ,,	3	2	—
♂U 96	× ,,	2	—	—
♀U 100	× ,,	6	—	3
♀U 101	× ,,	7	2	—
♀U 157*c*	× ,,	2	—	—
♂U 159*a*	× ,,	1	2	—
♂U 184	× ,,	—	3	—
♀U 231	× ,,	4	—	—
♀U 232	× ,,	—	3	3

Animals homozygous for **S** should give only offspring of the D.T.S. or D.D. (= Deep Dutch) classes, but animals heterozygous for **S** would be expected to give also offspring of the Mock Dutch (D.) class. Four of the animals which we suspected to have been heterozygous for **S** were tested in this way. Two of them, ♀ U 100 and ♀ U 232, gave some Mock Dutch as well as darker offspring. The other two, ♀ U 157*c* and ♂ U 159*a*, gave only darker progeny, but the numbers from each are so small that the result cannot be regarded as conclusive. The other six animals tested in this way, as shown in Table IX, gave only animals with much pigment varying from the higher Deep Dutch grade towards self. There is therefore no evidence against these six having been homozygous for **S**, though they may have been heterozygous for **T**.

Four of the dark F_2 animals were also crossed with Typical Dutch, as shown in Table X.

TABLE X.

	A.S.	D.T.S.	D.D.
♂U 97 × Dutch (**ppSSTT**)	—	7	—
♀U 98 × „	4	3	—
♀U 99 × „	—	7	—
♀U 101 × „	—	2	3

From F_2 animals homozygous in **S** we should look for offspring of the D.T.S. class, and in two cases these only were obtained. ♀ U 101 gave D.D. as well as D.T.S. offspring and was therefore probably heterozygous for **S**. An unexpected result was given by ♀ U 98, an animal which, for reasons given above, we suspect to have been heterozygous for **S**. Not only did she give no D.D. offspring, but four of her offspring were classed as nearly self. We can only suppose that sometimes an animal of the constitution **PpSSTT** is nearly self coloured in appearance.

The Self-coloured Rabbit.

Since the evidence must be considered conclusive that animals of the constitution **PPSSTT** always show some trace of white[1], even though this may be exceedingly faint, the question arises as to what the self-coloured rabbit is from a genetical point of view. In our opinion the complete disappearance of white is generally due to the action of **P** upon some grade of Dutch higher than that of Typical Dutch. Castle had a strain of Dutch which he described as "Tan" Dutch owing to the fact that it originated from a cross between yellow Dutch and Black and Tan. The great majority of these animals belonged to grades 3 and 4 of Fig. 1, *i.e.* were very near to our Deep Dutch. But they differed in the blaze being wider, and in there being more white on the nose than in animals of a similar grade classed by Castle as "Dark Dutch" and by us as **PP** or **Pp** animals. Indeed to judge from the photograph on Pl. II of Castle's paper they had the head and ears of Typical Dutch associated with the grade of pigmentation over the rest of the body characteristic of our Deep Dutch. Moreover, as Prof. Castle kindly stated to one of us in a letter, Tan Dutch may sometimes show *heterochromia iridis*. We regard these Tan Dutch of Castle as a higher grade

[1] This statement is made only for the material with which we have worked. Some of Castle's data point to the **PPSSTT** animal being self coloured. We incline to think that this discrepancy in the two sets of experiments is due to the fact that Castle's white Dutch animals were, on the whole, of a rather higher grade of pigmentation than our own—that the factors **P**, **S**, and **T** were in his case working on a rather more highly pigmented basis than in our own. The combined action of these three factors, in many of Castle's rabbits just brought about the elimination of the last trace of white, whereas in our own animals they just failed to do so.

in the true Dutch series, and lacking the factor **P**. Constitutionally we may represent them as **NNSSTT**, regarding **N** as a factor that turns a Typical Dutch into a Tan Dutch. Now if **P** were added to a rabbit of this constitution we should expect it, at any rate in the homozygous state, to turn it into a completely self-coloured rabbit. This, on our view, is what Castle actually did in an experiment involving a cross between his "Dark" and "Tan" Dutch. He found that F_1 animals were, as a group, darker than either of the parental groups, and might even be self coloured; while in F_2 a large proportion of self-coloured animals appeared. At the same time, the F_2 range was well beyond that of either parental group, animals as low as grade 11 making their appearance (cf. Castle, 1919, pp. 13–14, and Text-fig. 5). On the supposition that **P** was carried by the Dark Dutch, though not by Tan Dutch, this result is what we should expect. Moreover the results of the cross between Tan and White Dutch as described by Castle (*loc. cit.* p. 13 and Text-fig. 4) bear out this interpretation. For the cross gave an intermediate F_1, and an F_2 generation ranging between grades 3 and 14, as would be expected on the supposition that the Tan Dutch lacked **P**.

Hence we regard a self-coloured breed as commonly one that is homozygous for **P** on a basis of Tan Dutch, and in constitution normally **PPNNSSTT**, though it is possible that such animals may often be heterozygous for one or other of the factors **N**, **S**, and **T**. Such heterozygosity may doubtless be held accountable for the white marked animals that sometimes appear in strains of self-coloured animals, and more often after crosses between different strains of self-coloured rabbits, such as was recorded by Häcker (1915) from a cross between Himalayan and Black and Tan.

But although we consider the self-coloured rabbit generally to be of this nature we realise that there are other possibilities. For, having regard to Pap's results, it is probable that even higher grades than Tan Dutch may exist in the true Dutch series which lacks **P**. There is for instance a rare breed called the "St Nicholas" rabbit, occasionally seen at shows in this country. Here the white appears to be limited, at any rate in the show type, to the muzzle, blaze, and tips of the fore-paws. Among the few St Nicholas rabbits that we have seen at shows one exhibited some *heterochromia iridis*. In view of the fact that among all the many rabbits containing **P** which we have bred, not one showed any trace of *heterochromia*, we consider this good evidence for the lack of this factor from the St Nicholas rabbit. Consequently we must regard this rabbit as a grade of true Dutch even higher than the "Tan" Dutch,

and it is likely that such an animal, when only heterozygous for **P** would give rise to self colour. Whether the series of true Dutch can be extended to an even higher grade, even to self colour itself as claimed by Pap, we are at present doubtful. For we do not consider that Pap's facts exclude the possibility that the factor **P** entered into his material, and that to its interaction with other factors were due the self-coloured animals that appeared in the course of his work.

Conclusion.

As the result of earlier work, and of the experiments recorded in this paper, it is clear that the variety of white markings in the Dutch series of rabbits, ranging from almost white to self-coloured, can be interpreted in terms of four definite factors, **N**, **P**, **S**, **T**. Of these, **P**, **S** and **T** are transmitted independently, and it is probable that this is also true of **N**. We have found no evidence of linkage between any of the three that have come into our investigations. Nor again can they be regarded as members of a series of multiple allelomorphs in the way that Castle has suggested. Against such a view the evidence is conclusive.

Although the simple interpretation we have offered covers the essential features of the case, we fully recognise that there are points on which we can offer no adequate explanation. Such a point is the variation, sometimes considerable, in the markings of animals of similar constitution in respect of the three factors which we have distinguished. It is likely, as we have hinted, that there may exist other different factors influencing the pattern, though in a minor degree. The question of mismarking again, with the asymmetry of pattern involved, we have left practically untouched. Whether regularity and evenness of marking depend upon definite factors, or whether they are merely the chance results of differences in the early intrauterine environment, we do not know.

The experiments recorded in this paper have been carried out by means of the funds provided by the Development Commissioners for breeding research work with small animals.

APPENDIX.

A. WHITE DUTCH (PEDIGREE NO. 4).

As White Dutch (V.R.S.D.) we have classified such animals as are approximately of grades 16–17 in Fig. 1. Such animals may occasionally throw a slightly more pigmented form, as represented by grade 15, but generally they may be said to breed true with relatively little variation. On this point our results agree closely with those of Castle, though his White Dutch were on the whole rather more pigmented than our own. Owing to difficulties attendant upon close inbreeding we have not attempted to keep a pure line of White Dutch, but have made use of animals extracted in various ways from our mixed material. The relations of the various White Dutch used may be gathered from Pedigree no. 4. From time to time such animals have been mated together, and in no instance have they produced anything higher than that shown as grade 15 in Fig. 1, and it is only rarely that an animal has reached this grade. Nevertheless there are occasions when this has occurred (cf. ex ♀ T 102 in Pedigree 4) and the animal classed as $\frac{\text{R.S.D.}}{\text{V.R.S.D.}}$ Since our hypothesis demands that such a rabbit should be heterozygous for **T**, we must suppose that sometimes an animal of the constitution **ppssTt** falls into grade 16 rather than into grade 15, and is classed as White Dutch with the presumed constitution **ppsstt**. Probably ♀ T 102 was such an animal since she produced some young of this rather higher grade when bred to two different White Dutch bucks. Apart from this the White Dutch form does not call for any special comment.

B. SPOTTED DUTCH (PEDIGREE NO. 5).

Since Spotted Dutch animals of different grades, down to White Dutch, appeared in F_2 and subsequent generations from the original cross between Typical Dutch and Himalayan, it is probable that one or more of the original Dutch stock were in reality Mock Dutch (*i.e.* **Ppsstt** or **PpssTt**). Since the earlier work from 1907–12 was concerned with coat colour, the stock was bred as far as possible free from white markings, and it was not until 1912, when we started experiments on weight, and crossed Flemish with Spotted Dutch, that we set out to learn something of the nature of the pattern. Especially were we at that time interested in the heterochromic eye which is so commonly

found in animals of the Spotted Dutch and lower grades. Such Spotted Dutch and lower grade animals as were bred, were bred chiefly with the idea of ascertaining whether *heterochromia iridis* followed any definite scheme in transmission. As shown in Table X A, the earlier animals used by us were clearly carrying White Dutch in many cases.

TABLE XI.

			S.D.—R.S.D.	$\frac{\text{R.S.D.}}{\text{V.R.S.D.}}$	V.R.S.D.
A	♀G 33 (R.S.D.)	× ♂G 32 $\left(\frac{\text{R.S.D.}}{\text{V.R.S.D.}}\right)$	6	1	4
	♀G 34 (R.S.D.)	× ,,	4	1	—
	♀G 71 (R.S.D.)	× ♂G 76 (V.R.S.D.)	5	1	7
	♀G 70 (R.S.D.)	× ♂G 54 (R.S.D.)	6	—	6
B	♀G 63 (R.S.D.)	× ♂G 54 (R.S.D.)	5	—	—
	,,	× ♂G 174 (R.S.D.)	5	—	—
	♀Q 85 (R.S.D.)	× ♂Q 86 (R.S.D.)	3	1	—
	♀Q 88 (R.S.D.)	× ,,	10	1	—
	♀Q 111 (R.S.D.)	× ♂Q 117 (R.S.D.	4	—	—
	♀Q 128 (R.S.D.)	× ,,	6	1	—
	♀Q 150 (R.S.D.)	× ♂Q 149 (R.S.D.)	7	—	—

The remainder of the animals shown in Table X B, when bred together did not produce any V.R.S.D., though three out of the 43 young ones bred are recorded as intermediate between R.S.D. and V.R.S.D. It is possible that some of the Spotted Dutch were heterozygous for **S**. At this stage in the experiments the animals were not graded with the attempt at accurate subdivision made in our later efforts, when we classed our material in the four grades S.D., R.S.D., $\frac{\text{R.S.D.}}{\text{V.R.S.D.}}$, V.R.S.D. Nevertheless they show that Spotted Dutch animals can be got to breed reasonably true, without throwing either Typical Dutch or White Dutch. The more recent data shown in the last four generations of Pedigree no. 5 may be set out here as follows:

TABLE XII.

		S.D.	R.S.D.	$\frac{\text{R.S.D.}}{\text{V.R.S.D.}}$	V.R.S.D.
♀Q 111 (R.S.D.)	× ♂Q 117 (R.S.D.)	3	1	1	—
,,	× ♂R 17 (R.S.D.)	—	3	—	—
♀Q 232 (R.S.D.)	× ♂Q 231 (R.S.D.)	3	1	—	—
♀R 41 (S.D.)	× ♂R 39 (S.D.)	4	1	—	—
,,	× ♂Q 231 (R.S.D.)	1	3	—	—
♀R 85 (S.D.)	× ♂R 143*a* (R.S.D.)	2	3	—	—

Noticeable is the fact that two animals of the rather lower grade, classified as R.S.D., may sometimes give animals of the rather higher grade (S.D.) when bred together. On the hypothesis we have put forward we might explain this by supposing that the different animals

varied in constitution with respect to **S** and **T**: that while most classed as R.S.D. were **ssTT** some might be **SsTt**. Consequently some higher grade animals, **SsTT**, might arise, and also occasional lower grade ones, **ssTt**. We do not however wish to stress this suggestion because we do not consider the data sufficiently critical. A larger and better planned series of experiments would be necessary to unravel these complications, and these we did not undertake because we felt that our means were better employed in carrying out the experiments recorded in the body of this paper. What we wish to emphasise here is that the data are on the whole in accordance with the view that we were concerned with two kinds of Spotted Dutch animals, a darker and a lighter, either of which could have been got to breed fairly true.

C. TYPICAL DUTCH (PEDIGREE NO. 6).

Below is set out the evidence relating to the Typical Dutch strain which we have referred to in the account of our experiments. The animals to which reference is made in Table XIII below, will be found recorded in the lower half of Pedigree no. 6 (p. 412).

TABLE XIII.

	Mismarked Dutch	Good Dutch	White marked Dutch
♀Q 141 × ♂Q 176	—	4	4
,, × ♂Q 228	—	—	7
♀Q 177 × ♂Q 176	2	—	2
♀Q 238 × ♂Q 236	3	5	1
,, × ♂Q 176	3	9	9
♀Q 237 × ♂Q 236	4	3	2
,, × ♂Q 176	1	1	2
♀Q 229 × ,,	6	6	3
♀R 45 × ,,	5	6	—
♀T 52 × ♂T 155	2	4	12
	26	38	42

The 7 ♀♀ and 4 ♂♂ used as parents were all good typical Dutch of the type shown on Pl. XV, figs. 1–6. The offspring, however, were not all exactly like the parents, but could be divided into 3 classes, viz. good Dutch, mismarked Dutch, and Dutch with some white marking in the lumbar region. Mismarked Dutch may be described as typical animals in which pigmented patches were present on the normally white area. Generally these patches were relatively small as in R 45, shown on Pl. XIV, fig. 6; but occasionally the patch might be very large as in Q 229 Pl. XIV, fig. 5, and the animal, viewed from the side on which the patch occurs looks like an animal that is almost self coloured. Viewed from the other side however it was a typical Dutch in appearance. In the

other class there was a variable amount of white in the lumbar region (cf. Text-fig. 3). There might be hardly more than a trace, or, at the other extreme, it might spread out into a broad transverse band as in R 16 shown in Pl. XIV, fig. 4. Even when found at its maximum development it was not accompanied by any appreciable reduction of the coloured areas on the head and ears, such as occurs in Spotted Dutch. Nor did we find that these white marked Dutch threw any Spotted Dutch in the one instance in which they were bred together, *i.e.* ♀ P 201 × ♂ P 214 in Table XIV. But when mated together they

TABLE XIV.

	Mismarked Dutch	Good Dutch	White marked Dutch
♀P 201* (**Xxyy**) × ♂P 214* (**xxYy**)	—	3	19
♀P 200 (**XxYy**) × ,,	1	11	18
♀R 16* (**Xxyy**) × ♂Q 176 (**XxYy**)	—	3	2
♀T 51* (**Xxyy**) × ,,	—	—	5

* Denotes an animal with white markings.

throw a high proportion of white marked animals; and, as Table XIV also shows, they give a higher proportion of white marked animals when mated with good Dutch, than do these latter when bred together. It is worthy of note that in only one case did a mismarked Dutch appear among the 62 offspring bred from these white marked animals. This animal, together with the rest of the litter in which it occurred, is shown in Fig. 5.

The explanation of this variability within the Typical Dutch strain is not very obvious, and it is with some diffidence that we venture to offer the following suggestion. Let us assume the existence of two factors **X** and **Y**, both of which must be present in a "good" Dutch. When either one only, or neither is present the animal shows white markings. "Good" Dutch must be supposed to be normally heterozygous for both **X** and **Y**. Animals containing both **X** and **Y** and homozygous for **X** must be supposed to be "mismarked" Dutch, while animals containing both factors and homozygous for **Y** must be supposed to be either slightly mismarked, or else "good" Dutch in appearance.

From "good" Dutch therefore bred together the group "mismarked" and "good" should be to the white marked as 9 : 7. The actual figures in Table XIII are 64 : 42, where expectation is 60 : 46.

White marked Dutch bred together should usually give either white marked alone, or else "good" and white marked in the ratio 1 : 3. The actual figures from ♀ P 201 × ♂ P 214, the only mating of this type (Table XIV), are 3 good and 19 white marked.

Assuming the **xxyy** animals to be those with the greatest amount of white, from none of which we have bred, the usual white marked Dutch would be either **Xxyy** or **xxYy**. As we generally chose those with the least amount of white, and as we postulate a greater effect on pigment production for **X** than for **Y** the animals used for breeding must be supposed to have generally been **Xxyy**. But P 214 was probably **xxYy**

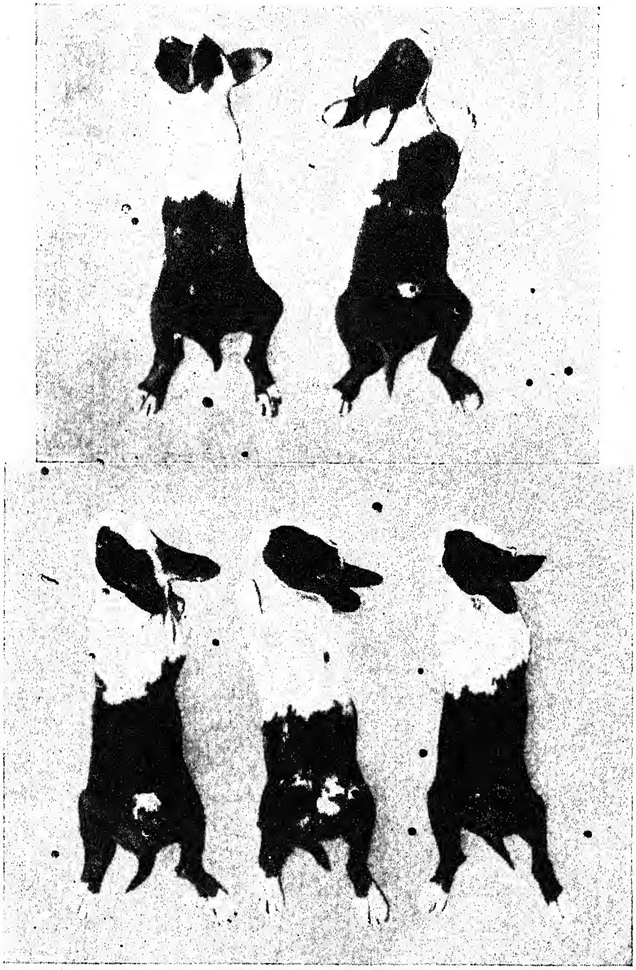


Fig. 5. Illustrating a litter from ♀ P 200 × ♂ P 214. Of the five young shown, three have definite white lumbar markings, and one of these is mismarked on the right side. The other two were reckoned as good Dutch, though a faint trace of white is to be seen in each. We have noticed that such faint traces tend to disappear as the rabbit grows older.

since he is recorded to have had a good deal of white marking, while P 201 had only a small amount and was probably **Xxyy**. This would explain the appearance of some "good" Dutch among the progeny of this pair, though 5 were to be looked for where only 3 occurred.

From the mating between ♀ P 200 and ♂ P 214 we should expect equal numbers of "good" and white marked. With one exception only these two classes appeared, though the white marked were rather in excess of expectation (cf. Table XIV).

The last two matings in Table XIV must be supposed to be of similar nature, viz. **Xxyy** and **XxYy**, and from them we should expect the three classes "mismarked," "good" and "white marked" in the ratio 1 : 2 : 5. The data are too scanty to test the point, but the actual figures 0 : 3 : 7 are not at variance with this interpretation.

Whether this prove to be an acceptable explanation or not, we must recognise that our strain of Typical Dutch is subject to variation, though these variations are not of a nature to lead us to confuse the animals belonging to it with either Spotted Dutch on the one hand, or Deep Dutch on the other.

In favourable cases we have been able to recognise the white lumbar marking in Spotted Dutch rabbits (*e.g.* R 18 shown on Pl. XX, fig. 4), but where the pigment becomes more reduced, as in the R.S.D. type, we should hardly expect to recognise it, even if it were present. Nevertheless the fact that the typical Dutch which we used normally throw such lumbar markings, must have introduced another element of complexity into the two series of experiments where Typical Dutch was crossed with White Dutch and Deep Dutch respectively. Although none of the F_1 animals showed white lumbar markings they reappeared at times upon F_2 animals, as would be expected if some of the F_1 animals carried the character, and these happened to be mated together. Again, though the white markings would rarely be recognisable as such on the various grades of Spotted Dutch they might nevertheless produce an effect sufficient to lead to the animal being classed in a grade different to that in which it would have been classed had the character not been present.

One further experiment in connection with Typical Dutch may be mentioned here. During war time we often used to lend the services of our buck rabbits to those who had does they wished to breed from. On one occasion a black doe with some white marking (of about grade 3 in Fig. 1), was mated with ♂ P 214. She gave only two kinds of offspring, viz. those with a little white marking and Typical Dutch, all of which

last were heterochromic in respect of eye colour. As the eye result was at that time of interest the doe (♀ Q 91) was purchased and mated again to P 214, and also to the White Dutch buck G 196. As shown in Pedigree no. 7 (p. 408) she gave with the former 11 Typical Dutch and 6 towards self colour; while with the latter she gave 2 R.S.D. and 1 near self colour. One of her Dutch daughters (♀ Q 51) was mated back to P 214, and gave 6 Dutch only. From two of these mated together (♂ Q 135 and ♀ Q 136), 7 Dutch and one animal recorded as "Spotted Dutch"[1] were reared. The series of facts points to ♀ Q 91 having been heterozygous for **P**, probably of the constitution **PpSSTT**, and is in accordance with our other experiments.

[1] In the light of what we learned subsequently about the white lumbar markings we suspect that this animal should have been more accurately classified as Dutch with excessive development of the white lumbar markings.

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EXPLANATION OF PLATES XIV—XXII.

In each case the record number of the animal is given. Where the animal figures in any of the pedigrees, this is indicated by the figure, or figures, in brackets after its record number.

Plate XIV.

Figs. 1–6 Examples of Typical Dutch rabbits bred in the experiments. Fig. 2 is a good example of *heterochromia iridis* in the left eye. Fig. 4 shows an unusually strong development of the white lumbar marking, which here forms a band reaching almost completely round the body. Figs. 5 and 6 are examples of heavily mismarked Dutch; in both cases the animal viewed from the other side appeared as a Typical Dutch.

Plate XV.

Figs. 1–6. Examples of Typical Dutch rabbits bred in the experiments.

Plate XVI.

Figs. 1–5. Examples of Mock Dutch rabbits bred in the experiments.

Plate XVII.

Figs. 1–6. F_1 animals from the cross Typical × Deep Dutch. Figs. 3 and 4 represent the average grade of pigmentation in such animals. Figs. 1 and 2 show extreme development of pigment, the more pigmented side being shown in each case. Figs. 5 and 6 represent the extreme development of white in animals of this class.

Plate XVIII.

Figs. 1–6. Almost self-coloured rabbits (A.S.), F_2 rabbits from the cross between Typical and Deep Dutch.

Plate XIX.

Figs. 1–4. Deep Dutch (**PPsstt**) rabbits. Animals of this constitution frequently show a strong tendency towards mismarking—a fact brought out in the examples illustrated. Fig. 4 shows an unusually heavy development of pigment on the left side.

Plate XX.

Figs. 1–6. Examples of Spotted Dutch (S.D.) animals. Fig. 4 shows a strong development of the white lumbar band in this type.

Plate XXI.

Figs. 1–2. Examples of White Dutch (V.R.S.D.).
Figs. 3–6. Examples of animals classed as Reduced Spotted Dutch (R.S.D.).

Plate XXII.

Illustrating the result of a mating between a Mock Dutch ♀ and a White Dutch ♂. Five each of the only two types of offspring produced are shown on the plate.

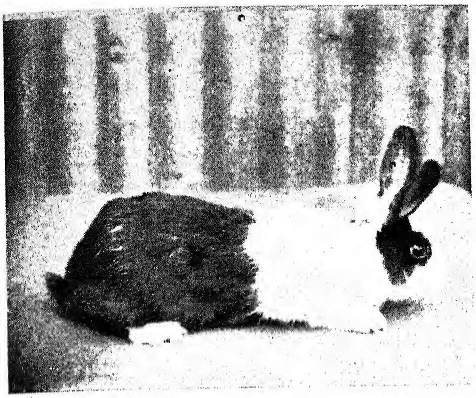


Fig. 1. R 32.

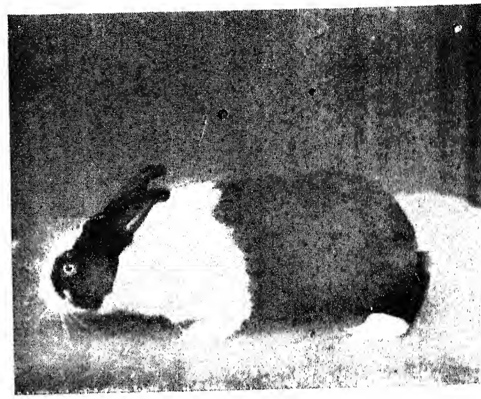


Fig. 2. Q 176 (*3*, *6*).

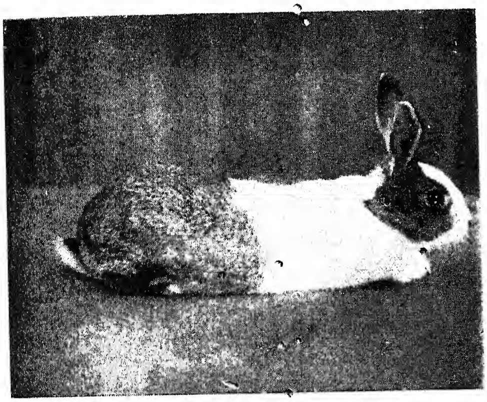


Fig. 3. Q 237 (*3*, *6*).

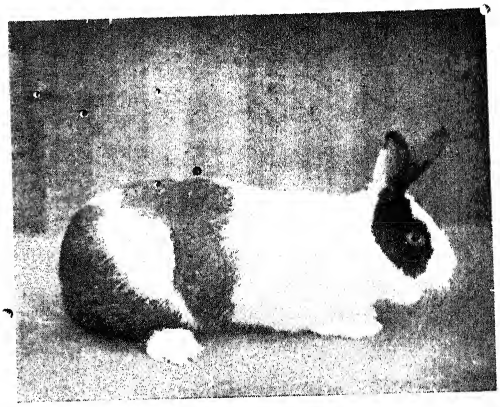


Fig. 4. R 16 (*6*).

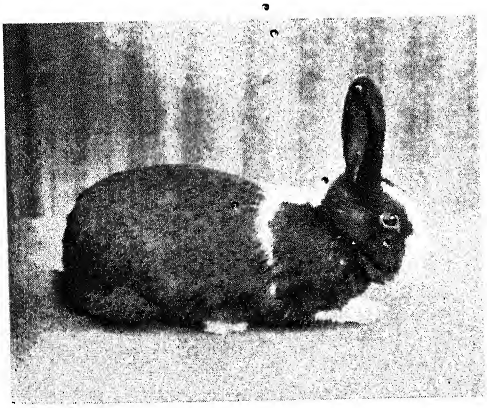


Fig. 5. Q 229 (*6*).

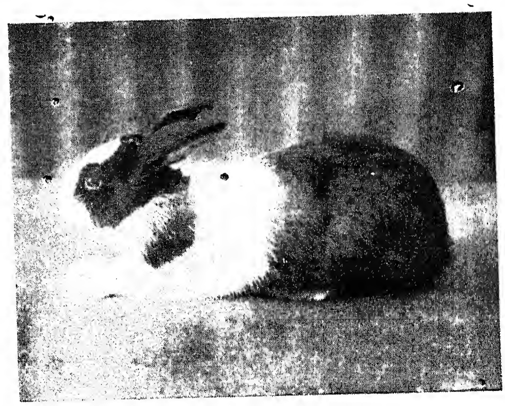


Fig. 6. R 45 (*3*, *6*).

TYPICAL DUTCH.

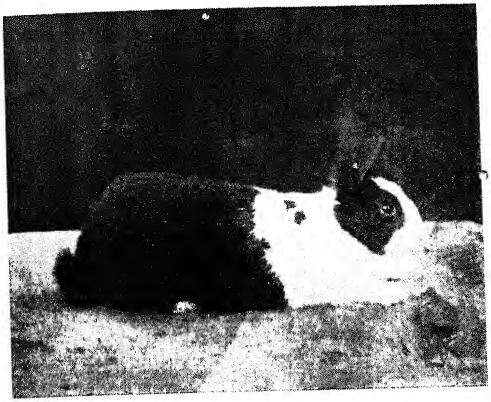


Fig. 1. W 26*b* (*6*).


Fig. 2. T 155 (*6*).

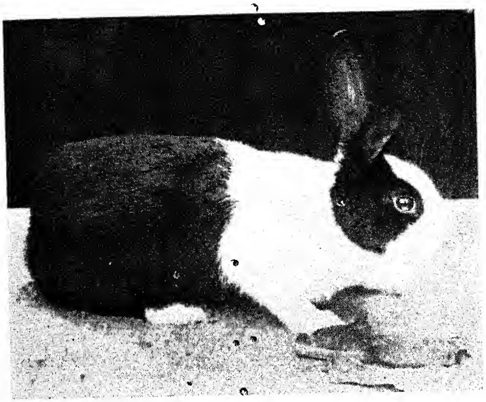


Fig. 3. W 26*a* (*6*).

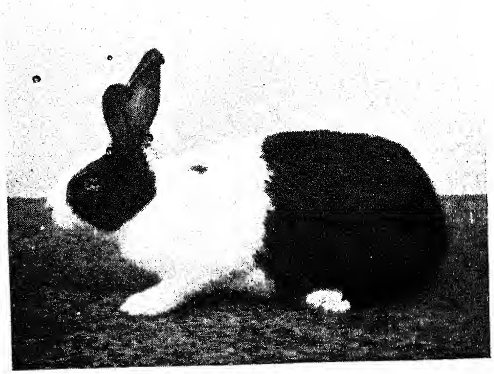


Fig. 4. T 51 (*3, 6*).

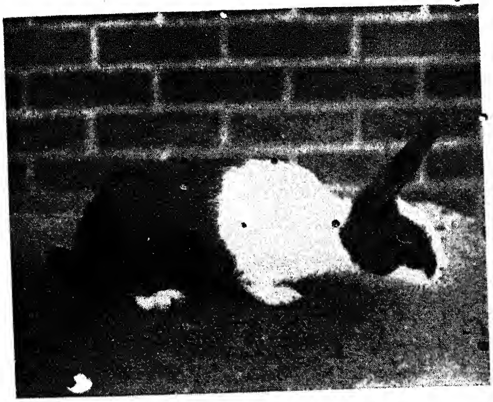


Fig 5. W 26*c* (*6*).

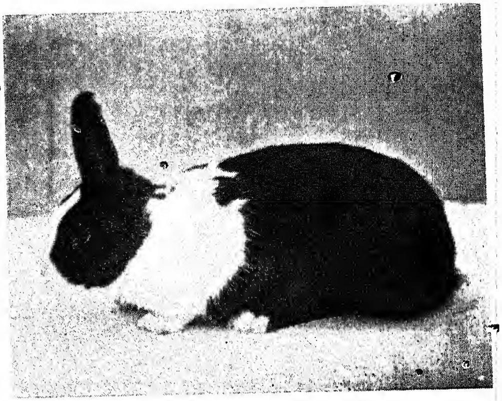


Fig. 6. R 43 (*6*).

TYPICAL DUTCH.

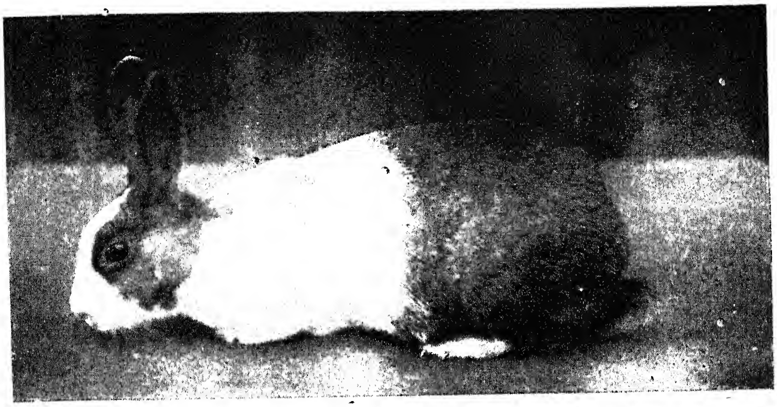


Fig. 1. Q 195 (*1, 2, 3*).

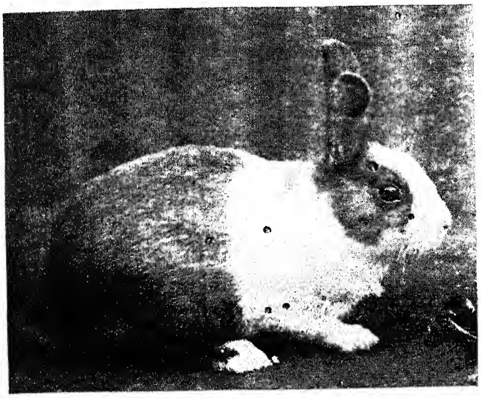


Fig. 2. R 240 (*1*).

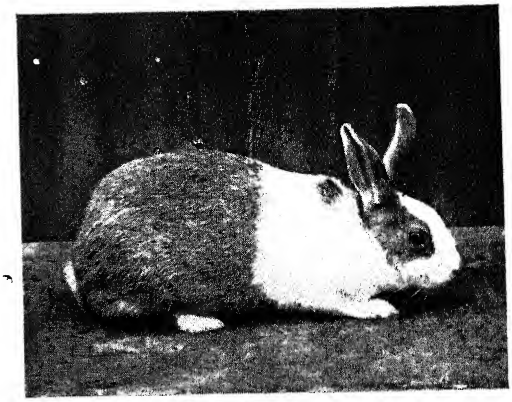


Fig. 3. R 206.

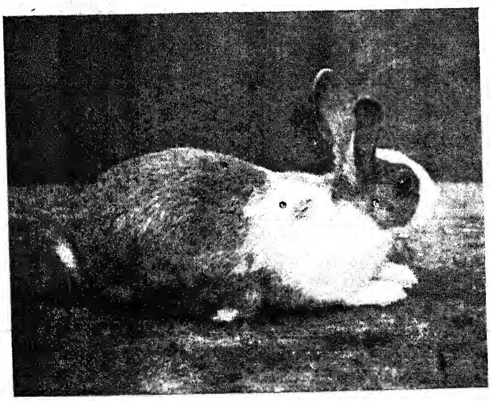


Fig. 4. R 99 (*1*).

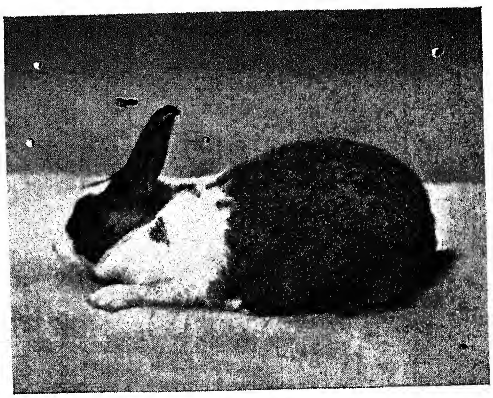


Fig. 5. R 20 (*1*).

Mock Dutch.

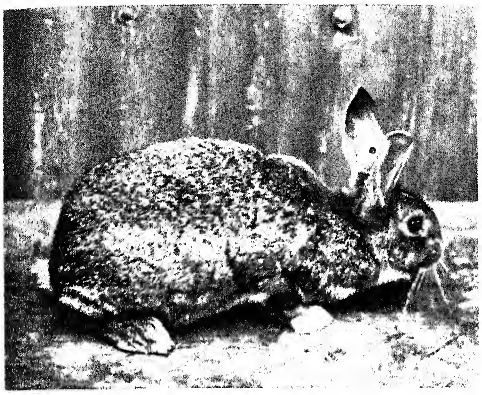


Fig. 1. T 177 (*3*).

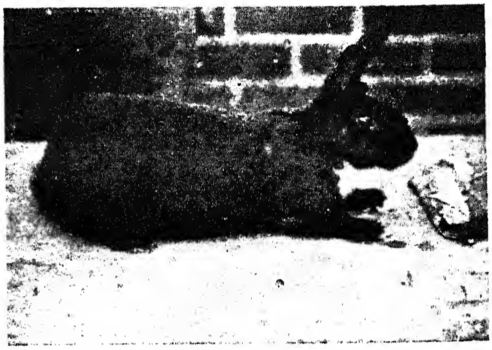


Fig. 2. U 233 (*3*).

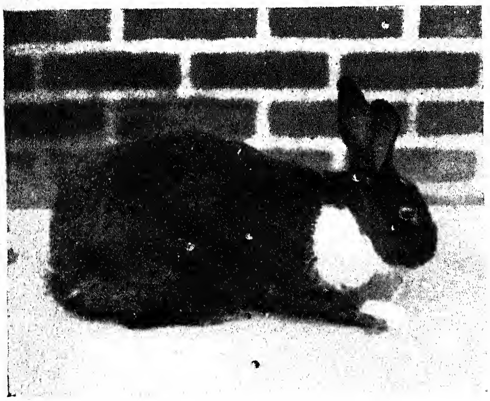


Fig. 3. U 234 (*3*).

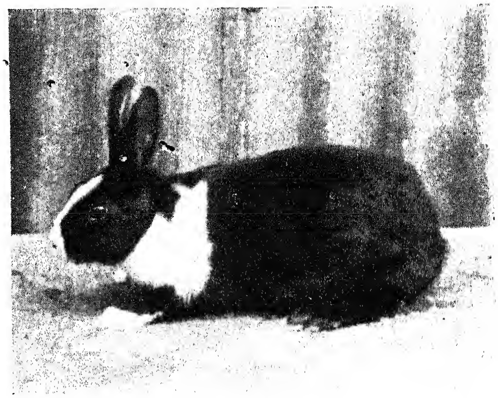


Fig. 4. T 42 (*3*).

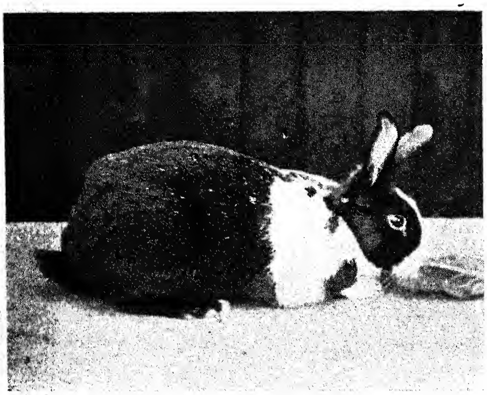


Fig. 5. T 35*b* (*3*).

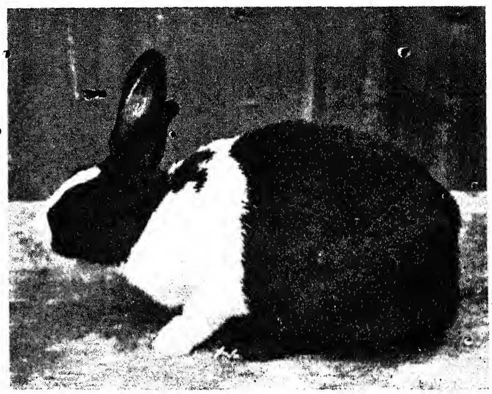


Fig. 6. T 79 (*3*).

F_1 ex Typical × Deep Dutch.

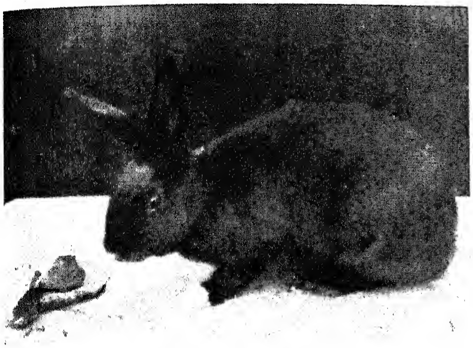


Fig. 1. U 96 (3).

Fig. 2. U 98 (3).

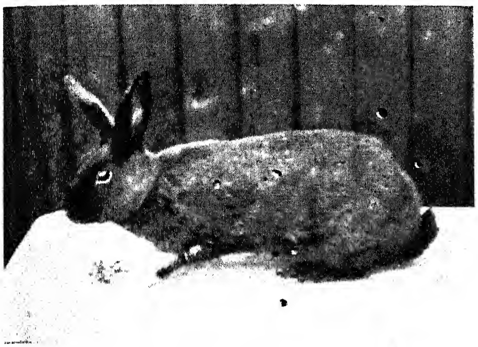


Fig. 3. U 74 (3).

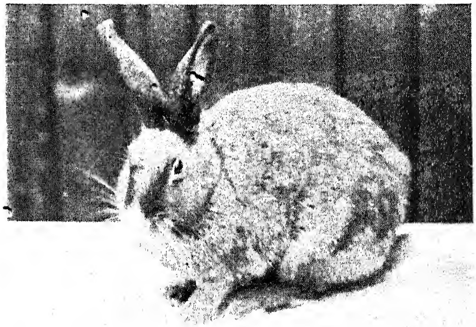


Fig. 4. U 63*b* (3).

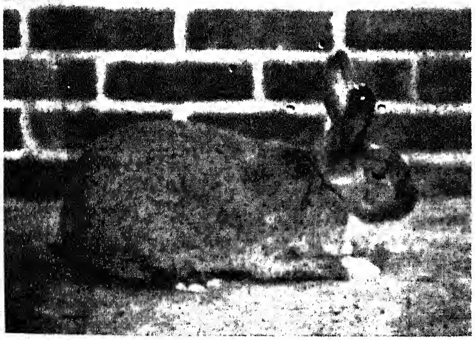


Fig. 5. U 184 (3).

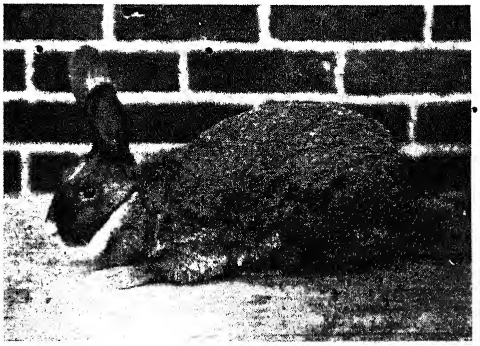


Fig. 6. U 100 (3).

Dark F_2 ex Typical × Deep Dutch.

Fig. 2. R 19 (2).

Fig. 4. T 95 (2).

Fig. 1. R 207 (3).

Fig. 3. T 92.

DEEP DUTCH.

PLATE XX

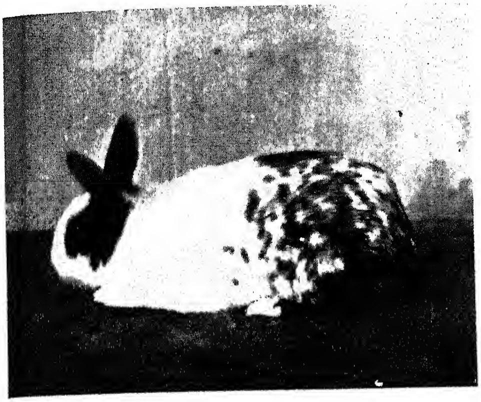


Fig. 1. Q 231 (5).

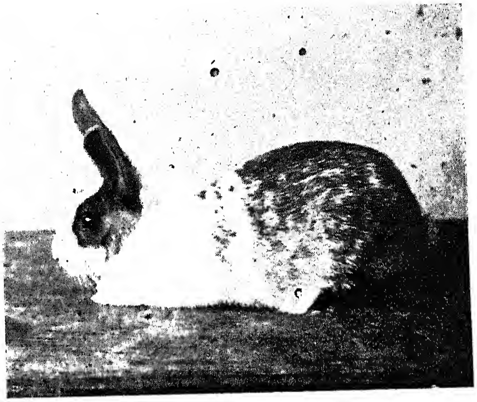


Fig. 2. R 39 (5)

Fig. 3. R 103 (5).

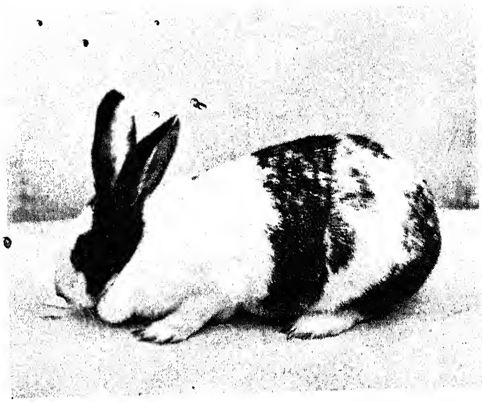


Fig. 4. R 18 (5).

Fig. 5. R 83 (5).

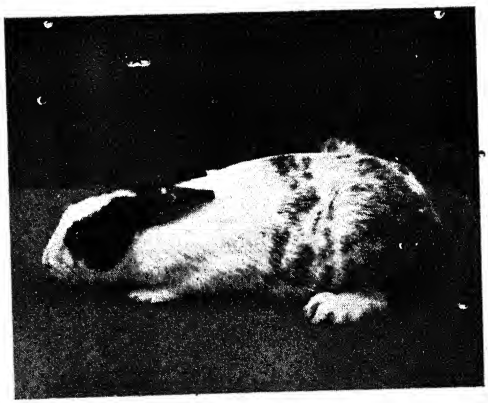


Fig. 6. R 33.

SPOTTED DUTCH.

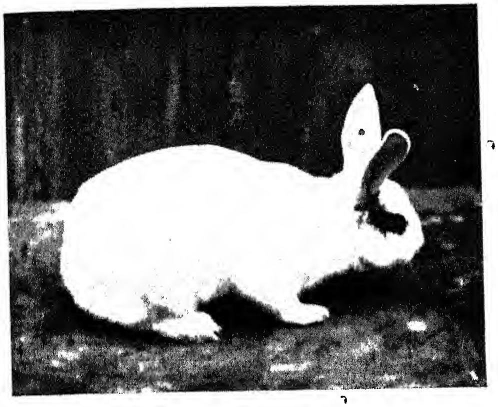


Fig. 1. T 161 (*4*).

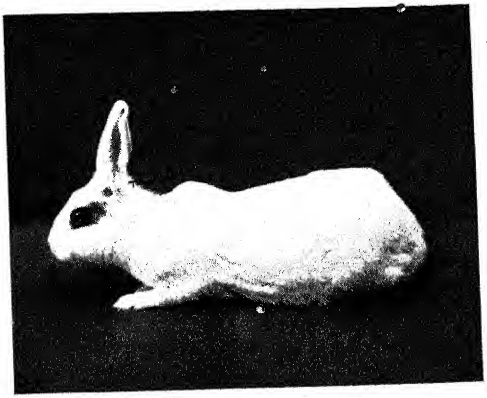


Fig. 2. R 181 (*4*)

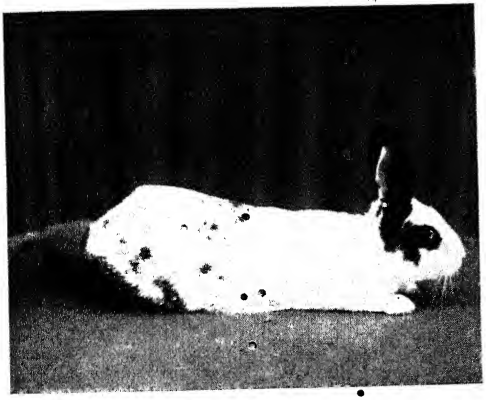


Fig. 3. R 85 (*5*).

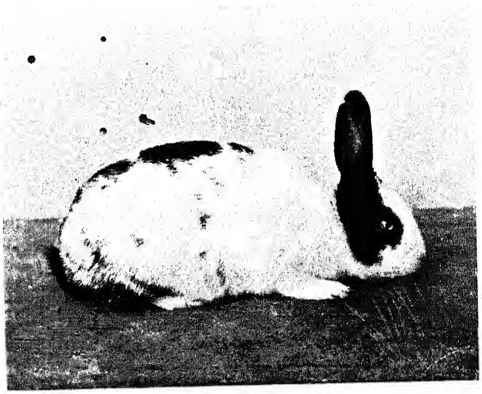


Fig. 4. R 17 (*5*).

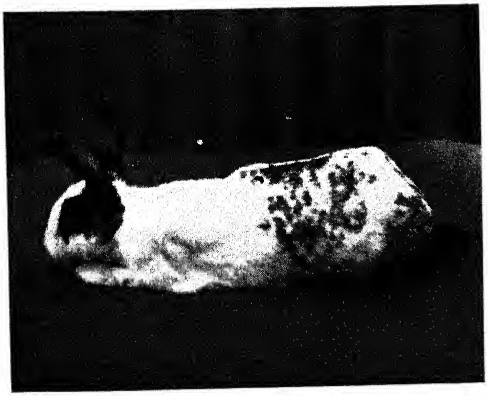


Fig. 5. Q 111 (*5*).

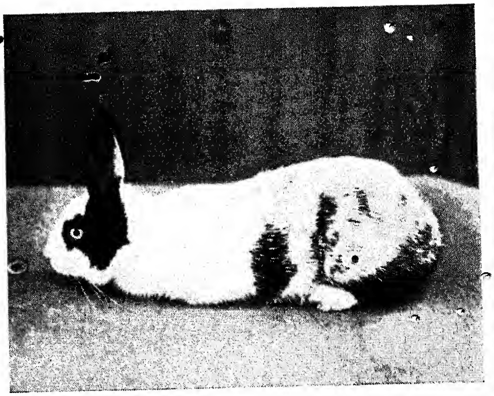


Fig. 6. R 34 (*4*).

White and Spotted Dutch.

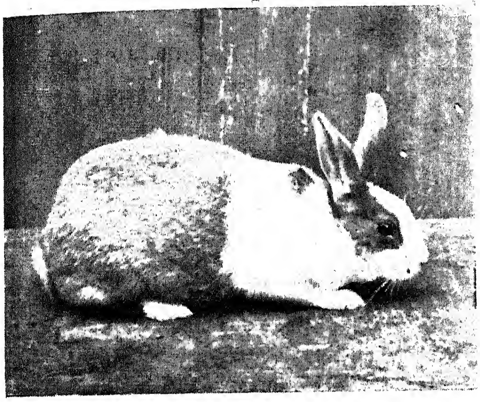


Fig. 1. R 206.

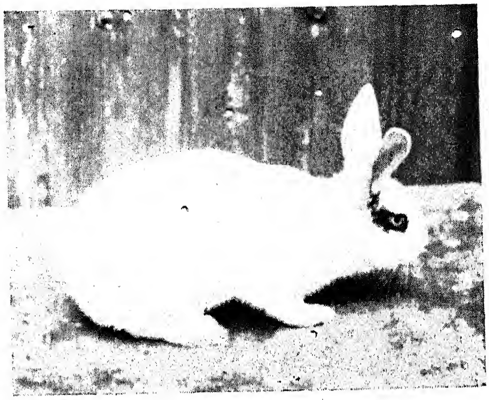


Fig. 2. T 161.

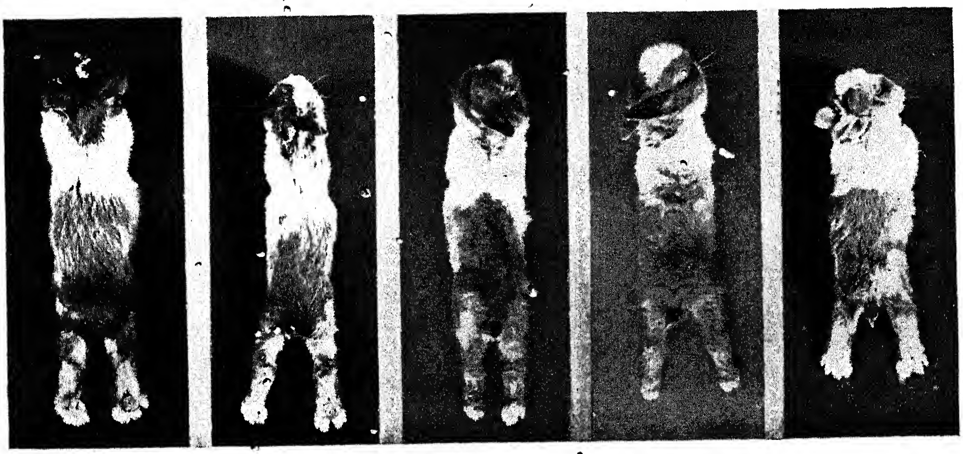


Fig. 3.

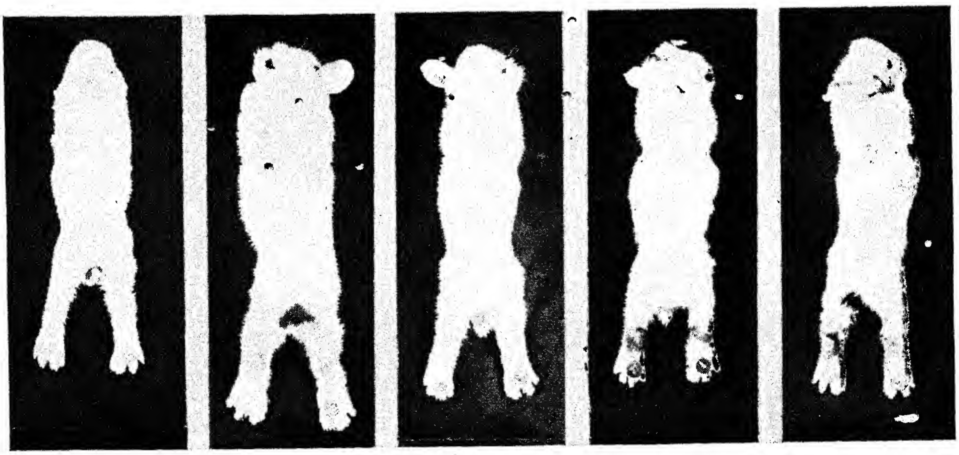
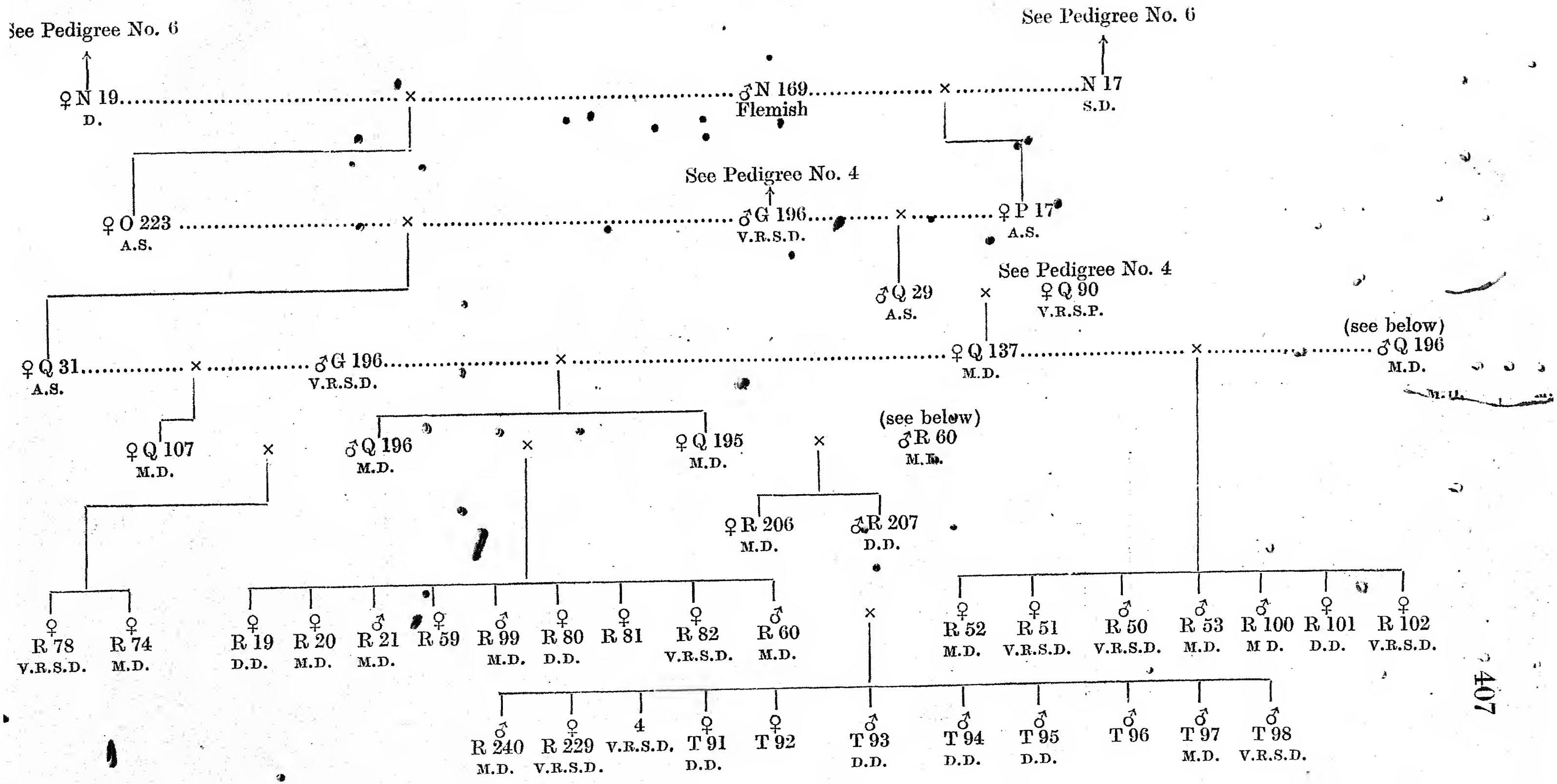


Fig. 4.

MOCK DUTCH × WHITE DUTCH.

PEDIGREE No. 1.

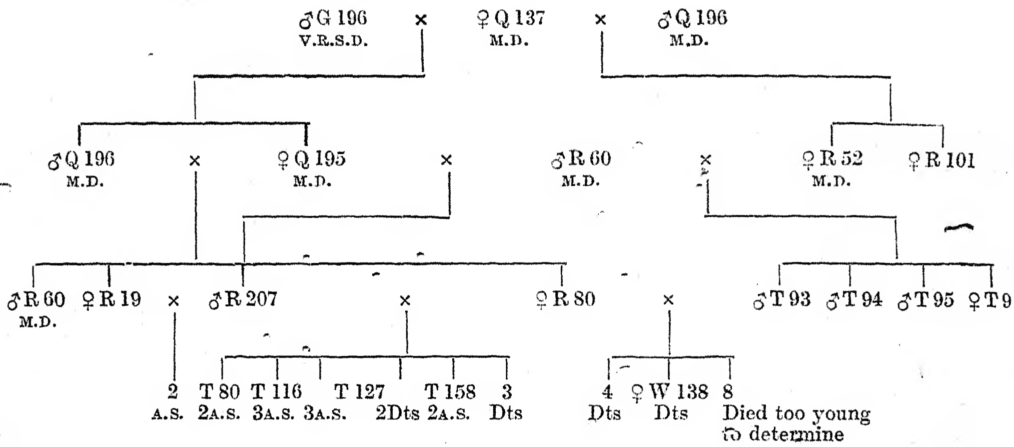
A.S. = Almost Self. M.D. = Mock Dutch. D.D. = Deep Dutch (homozygous for P).
(Other abbreviations as in text.)



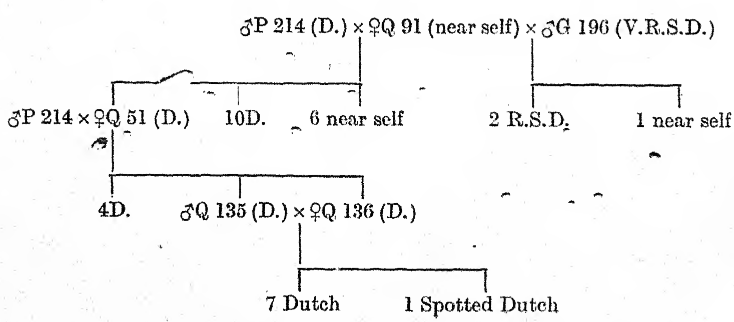
PEDIGREE No. 2.

The P^2 Pedigree.

(Unless otherwise designated the animals in this pedigree were homozygous for **P**.)

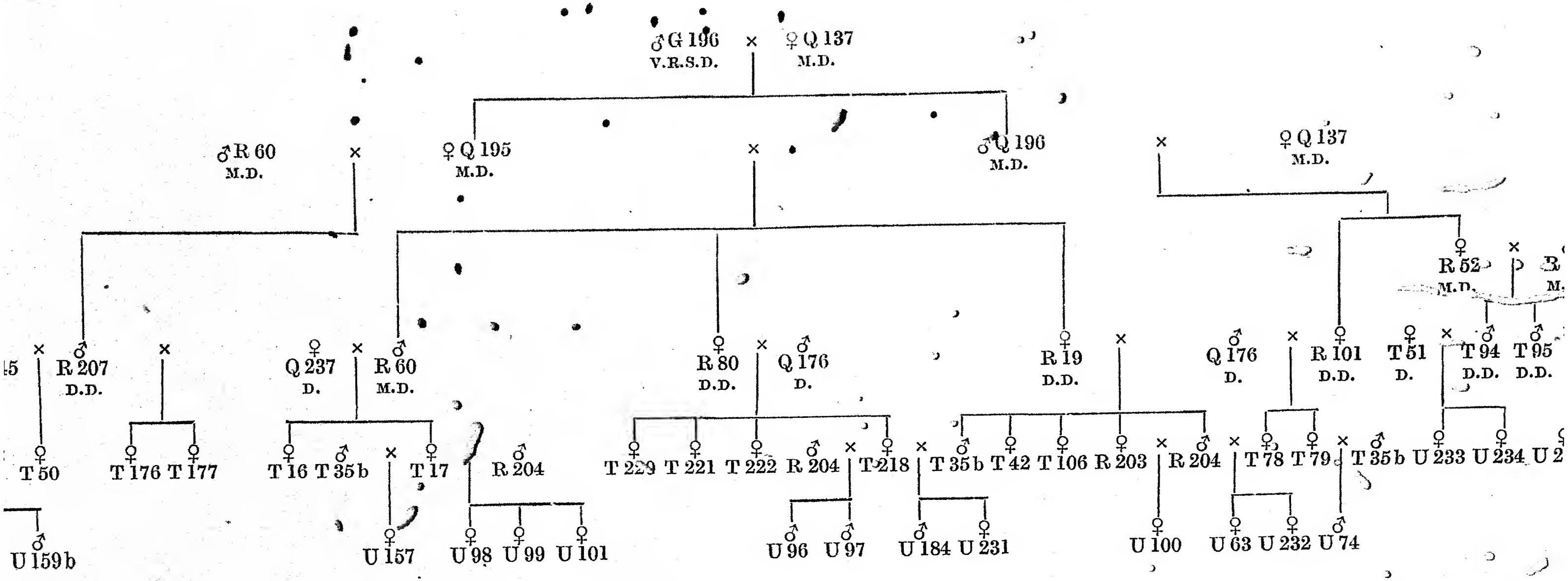


PEDIGREE No. 7.



PEDIGREE No. 3.

D. = Typical Dutch. D.D. = Deep Dutch. M.D. = Mock Dutch



PEDIGREE No. 4.

(= White Dutch Pedigree.)